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The Definition of "Species"

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On the cover: Two of the four Snake River sockeye salmon that returned to Redfish Lake, Idaho, in Fall 1991. NMFS photo by Joni Packard.

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Restricted Access vs. Open Access Methods of Management: Toward More Effective Regulation of Fishing Effort

JAMES R. WATERS

Introduction

This paper provides background information about why economists advocate limited entry as a method of fishery management. Its purpose is to give a general overview of the rationale for limited entry rather than a detailed account of existing programs. Townsend (1990) provides a review of existing limited-entry programs.

There are many criteria and objectives by which alternative methods of fishery management can be judged. For example, biologists are interested in the maintenance of adequate recruitment or improvement in recruitment, population age structure, and genetic diversity. Economists are interested in the long-term achievement of these goals in an economically efficient manner. Economic efficiency is loosely defined here as society's ability to maximize the combined value of commercial, recreational, and aesthetic products and services that can be obtained for a given level of cost, or the achievement of a given level of products and services at minimum cost. Economists advocate limited entry as a method of fishery management because economic efficiency is not likely to be achieved in an open-access fishery.

This paper is presented in five sections. The first section describes how unrestricted access to a fishery leads to inefficiency and overfishing. Unharvested fish are common property, which eventually creates a situation in which there are too many fishermen in the fishery, each applying too much effort. Excess capital and labor could be used elsewhere in a more cost effective manner and the same quantity of fish could be produced at lower overall cost.

The second section describes how open-access methods of regulation lead to further inefficiencies. Restrictions or prohibitions on the use of certain types of fishing gear, quotas, size limits, trip limits, and seasonal and area closures can achieve short-term biological improvements, but only by forcing fishermen to use more costly or less productive methods of fishing. The third section describes why, in the long term, unrestricted access tends to compromise the biological objectives of regulation. The potential long-term benefits of open-access regulations tend to disappear due to uncontrolled increases in fishing effort, all regulated to use economically inefficient methods of fishing. See Anderson (1986), Bell (1978), Crutchfield (1973), Crutchfield and Pontecorvo (1969), Crutchfield and Zellner (1963), Gordon (1954), Keen (1988), and Scott (1979) for further discussion.

Methods of limiting entry attempt to minimize the need to implement regulations that impose further economic inefficiencies. The fourth section summarizes some advantages and disadvantages of license limitation and catch rights as the two primary methods of restricting access to a fishery. Catch rights have better potential to improve long-term biological and economic benefits, provided that enforcement and monitoring costs are not too great. Section five summarizes the paper and discusses why managers of marine fisheries in the United States seem to prefer open-access regulations. Limited entry is generally considered to apply to commercial fisheries. This paper follows that supposition; however, section five speculates about the possibilities of applying limited-entry methods of regulation to recreational as well as commercial fisheries.

Open Access and Incentives to Overfish

Marine fisheries represent a modern version of Hardin's (1968) "tragedy of freedom in a commons" in which fishermen, each acting in his or her own self interest, are compelled to overfish and deplete the resources upon which they depend. Fish are said to be common property because no individual owns the ocean or the fish in it. Hence, fish may be harvested on a first-come-first-served basis by anyone with appropriate gear, subject

James R. Waters is with the Southeast Regional Office, National Marine Fisheries Service, NOAA, 9450 Koger Boulevard, St. Petersburg, FL 33702. Current address: Beaufort Laboratory, Southeast Fisheries Center, National Marine Fisheries Service, NOAA, Beaufort, NC 28516-9722.

ABSTRACT—This paper gives an overview of the economic rationale for limited entry as a method of fishery management and discusses general advantages and disadvantages of license limitation and catch rights as the two primary methods of restricting access to marine fisheries. Traditional open-access methods of regulation (e.g., gear restrictions, size limits, trip limits, quotas, and closures) can be temporarily effective in protecting fish populations, but they generally fail to provide lasting biological or economic benefits to fishermen because they do not restrict access to the fishery. The general result of regulation with unrestricted access to a fishery is additional and more costly and complex regulations as competition increases for dwindling fishery resources. Regulation that restricts access to a fishery in conjunction with selected traditional methods of regulation would encourage efficient resource usage and minimize the need for future regulatory adjustments, provided that enforcement and monitoring costs are not too great. In theory, catch rights are superior to license limitation as a means of restricting access to a fishery.

to existing regulations established by state and Federal governments as trustees of the public's resources. This creates a situation in which what is optimal for the individual fisherman is not always optimal for all fishermen combined.

The number of fishermen in a fishery tends toward an equilibrium in which the net revenues (after accounting for fixed and variable costs) earned by an additional fisherman just equal his opportunity cost, defined as the net income that could be earned in another fishery or another occupation[1]. Fishermen will enter a fishery if they expect to earn more than they could elsewhere; conversely, they will leave a fishery if they cannot earn as much as they could elsewhere. However, when a fisherman expands his effort or a new fisherman enters the fishery, he imposes what are called indirect or external costs on everyone else. These external costs represent the value of the additional overfishing created by his extra fishing effort and correspond to the negative component of utility in Hardin's (1968) example about overgrazing.

There are several types of external costs in a fishery. Crowding externalities reduce catch rates during the current harvesting season by distributing the available catch among a greater number of participants. Stock externalities reduce future catch rates by reducing the size of next year's fish population via reductions in fish survival and spawning potential.

A crowding externality occurs because fishermen harvest from a common pool of fish. Therefore, every new entrant into a fishery would capture some fish that would have been caught by his competitors (Bell, 1978; Cheung, 1970). Each fisherman may seem to have little or no effect on the catch rates of his competitors, but when fishermen simultaneously expand their fishing effort, the result is lower catch rates for all. In other words, the addition of fishing effort causes the fishery pie to be divided into smaller pieces. The commercial trap fishery for spiny lobsters in Monroe County, Fla., is a good example. The number of traps fished has tripled since the early 1970's while total harvest has fluctuated without trend.

A stock externality occurs because common property subverts the incentives to save fish for future harvest. By postponing the harvest of some fish, fishermen could invest in future fish supplies and future commercial income or recreational enjoyment. But few fishermen would voluntarily alter their harvesting techniques or strategies to conserve fish for the future because there is no assurance that the fish they save would not be caught, either now or in the future, by competing fishermen (Scott, 1955; Christy, 1978). Once again, each fisherman may have no noticeable effect on the size of the next year's fish population, but the simultaneous expansion of effort by all fishermen results in smaller populations of fish available for capture in the future. Fish like the deep-water groupers probably have significant stock externalities because they are relatively long lived, slow growing, and easily depleted.

The magnitude of external costs varies with the overall exploitation rate. When exploitation rates are low, expansion of fishing effort may have a negligible adverse effect on current and future catch rates. Overfishing may not occur or may not be severe. However, when exploitation rates are high, expansion of effort may have a considerable effect on current and future catch rates. The problem is that each fisherman receives the entire benefit of employing his additional fishing effort, but the additional, indirect effects of overfishing are dispersed among all fishermen. Although external costs are real, they occur mainly at the expense of other fishermen so that the individual has little incentive to curtail or alter his harvesting practices to avoid them. Hence, fishermen do not account for external costs in their decisions to enter or leave a fishery or to expand their scales of operation. The result is too many fishermen, each fishing too intensively[2].

The net addition to the value of output after accounting for external costs is less than the costs of employing the extra effort (Anderson, 1986; Cheung, 1970; Gordon, 1954), which implies that the resources used to produce excess effort would be more cost effectively employed in other fisheries or other sectors of the economy. The existence of significant external costs reflects what economists call "market failure" in which the normal competitive forces which affect the decisions of individual fishermen do not result in an optimal overall harvest from the perspective of society as a whole.

Although certain resources, such as some marine fishes, are scarce, they have remained common property because the costs of defining and enforcing a claim of ownership are higher than the expected benefits[3] (Cheung, 1970; Demsetz, 1967). Therefore, public regulation of marine fisheries appears necessary to overcome the incentives to overfish and its consequences. Limited entry attempts to overcome the problem of external costs and its built-in incentives to overfish through the creation and enforcement of property rights where they have not evolved naturally. More correctly, limited-entry systems of management introduce elements of property rights into a fishery through the issuance of what may be called fishing use rights, fishing privileges, or the right of access to the fishery. Limited entry does not assign ownership of the ocean or the fish in it.

Open-access Regulations Create Economic Inefficiencies

Traditional, open-access methods of managing a fishery attempt to reduce fishing mortality either directly (with gear restrictions or prohibitions) or indirectly (by restricting the allowable catches through the use of quotas, trip limits, size limits, and seasonal and area closures). These methods can work biologically, at least in the short term, but they create economic inefficiencies by forcing fishermen to adopt less produc-

[1] For example, consider the person who earns $30,000 per year as a hired captain on a company-owned fishing vessel. His next best employment alternative might pay only $20,000. That is, his opportunity cost is $20,000. If he were permanently unemployable elsewhere, then his opportunity cost would be $0.

[2] Other factors, such as government loan programs and tax law, may exacerbate the problem of overcapitalization in the fishery, but the tendency to overfish in the open-access (common property) fishery would remain even if those other factors did not exist.

[3] The benefits of private property rights depend on the ability to exclude others from using a resource if they are not willing to pay for its use. If it is too costly to exclude nonpayers, then common property prevails and fishermen are compelled to harvest as quickly as possible to keep up with their competitors.

tive, and hence less profitable, harvesting techniques and/or to incur higher costs to comply with or react to the regulations. Some economic consequences of traditional regulatory techniques are briefly summarized below. Anderson (1986), Bell (1978), Christy (1978), Crutchfield and Pontecorvo (1969), and Crutchfield and Zellner (1963) provide more complete discussions.

Gear restrictions and prohibitions tend to induce economic inefficiency by forcing fishermen to use more expensive and/or less productive fishing techniques. Fishermen could switch to other gear types, but presumably these fishermen were already using their most profitable gears, so the switch would reduce profits. Also, fishermen could increase their usage of uncontrolled components of effort. For example, if the number of lobster traps per boat were restricted, fishermen might reduce soak times, adopt faster trap pullers, or experiment with new trap designs or different baiting techniques. Or, fishermen could invent a new gear or fishing technique. Even if fishing mortality were initially reduced by gear restrictions and prohibitions, it would not necessarily be maintained at a reduced level because with open access there could be a long-term increase in the number of fishermen each using the restricted gear.

Annual quotas and the resultant seasonal closures encourage fishermen to seek more effective ways to maximize their shares of the overall catch before the quota is reached and the season is closed. Fishermen would fish more intensively earlier in the season and would actively seek out and adopt new gear, larger vessels, or different technologies designed to increase catches before the fishery is closed. Yet, catches per fisherman do not necessarily increase due to crowding and stock externalities and the overall limit on production. Hence, quotas and seasonal closures increase harvesting costs, reduce the length of the fishing season, and may reduce dockside prices because the entire industry's catch is landed during a shorter period of time. Also, a shorter fishing season could lead to an overall reduction in product quality if fish are not properly stored when boats are at sea during the race for fish, if a larger fraction of the overall catch must be frozen rather than sold in fresh markets, and if fish must be frozen for longer periods of time before they are marketed.

One reviewer questioned why gear restrictions/prohibitions and annual quotas are identified as creating additional inefficiencies if they spur innovation. Actually, there is nothing wrong with innovation per se. The inefficiencies arise when fishermen are compelled to adopt innovations which lead to premature capital replacement and overinvestment in fishing power for the expected harvest rate. The total commercial harvest will not be taken with minimum cost. In addition, more fishing power applied to an already stressed fish population would simply hasten the next round of regulations designed to restrict or prohibit the new technology.

Minimum size limits, another commonly used regulation, tend to reduce catch rates or increase harvesting costs in several ways. Normal commercial operations often preclude fishermen from promptly returning undersized fish to the water, which would tend to reduce the likelihood that fish survive when released, especially in deeper water. These fish are wasted because they do not contribute to current or future catches or to an enhanced fish population. Even if fish survive when released, fishermen incur extra costs to cull them from the rest of the catch. Fishermen may minimize their catches of undersized fish by using larger hooks or net mesh openings and by avoiding fishing grounds known to have large concentrations of small fish, but they would incur extra gear and fuel costs to do so. Some fishermen could use undersized fish for bait, thereby saving bait costs as well as extra gear and fuel costs, but this practice would deny the potential future benefits of the size limit. In addition, because size limits do not restrict access to a fishery, they would not prevent potential long-term increases in fishing effort, which would increase the proportion of fish harvested as soon as they reached the minimum legal size, with the ironic consequence that relatively few fish would survive to exceptionally large or trophy sizes.

Other open-access methods of regulation also increase fishermen's costs of harvesting a given quantity of fish. For example, seasonally closed fishing areas or permanently closed marine sanctuaries (Davis, 1989; Plan Development Team, 1990; Tisdell and Broadus, 1989) would eliminate current and future catches from the closed areas, and fishermen would incur increased travel costs to legal fishing grounds. Trip limits would force fishermen to make shorter but more frequent fishing trips, which would increase fuel costs and the amount of nonfishing time spent traveling from port to fishing grounds and back.

Open-access Regulations Cannot Control Long-term Increases in Fishing Effort

Although open-access methods of management can reduce harvest levels and may initially reduce fishing effort, none of them can control potential long-term increases in fishing effort. Commercial and recreational fishing effort is presumed capable of increasing over time. In the commercial sector, fishing effort is not fixed; capital and labor are observed to enter and leave the fishery for a variety of reasons, including changes in fishery regulations and changes in the profitability of participating in a particular fishery compared to alternative fisheries. While these factors could cause fishing effort to either increase or decrease, effort is expected to increase over time due to long-term increases in the population of consumers of commercial fishery products and cost-saving technological change. The demand for commercial fishery products will probably increase over time as the population of consumers and their incomes increase. In addition, cost-saving technological change enhances the profitability of fishing, which would attract more effort into the fishery. In the recreational sector, marine fishing activities have increased and probably will continue to increase due to increases in coastal populations, per capita income, tourism in coastal regions, and improvements to highways that facilitate travel to coastal areas.

If regulations such as gear restrictions, quotas, minimum size limits, trip limits, and closures were successful in enhancing stock biomass and, therefore, catch

rates and profits (for commercial fishermen) or utility (for recreational fishermen), fishing effort would be expected to increase. This increased effort would tend to compromise short-term biological gains that had been achieved, and eventually would require additional regulations to further control fishing mortality. Increased effort would also cause catch per unit of effort to decline due to the crowding and stock externalities described earlier. This leads to the phenomenon known as dissipation of fishery rent[4] in which potential long-term economic benefits of regulation tend to disappear as more effort enters the fishery. However, fishermen do not enter or leave a fishery at exactly the same time because their opportunity costs (i.e., potential incomes in alternative fisheries or land-based employment) are not the same for themselves or for their investments in boats and gear, and because their expectations differ about the future profitability of the fishery. Therefore, the potential benefits of regulation would be minimized but not completely eliminated (Anderson, 1985).

If traditional regulations proved ineffective and fish stocks became depleted and catch rates declined, fishermen could leave the fishery in search of more profitable fisheries or other employment. On the other hand, fishermen could maintain or even increase their levels of participation in a fishery if increases in demand and cost-saving technological change kept financial returns at acceptable levels despite a declining fish population (Bell, 1978; Christy, 1978). For example, ex-vessel prices for red snappers in the multi-species reef fishery of the Gulf of Mexico have increased over time due, in part, to an increased demand by consumers, a deteriorating domestic red snapper population, and loss of fishing privileges in foreign waters. In addition, fishermen have received higher prices for groupers and other (than red) snappers as consumers increased their demand for substitute species in response to higher red snapper prices. Thus, fishing has remained profitable although red snappers represent a declining share of the overall catch of reef fish.

The usual result of regulation with unrestricted access to a fishery is more and increasingly restrictive regulations as competition increases for dwindling fishery resources. Each regulatory adjustment offers temporary relief to the fish population, but over time additional effort likely will create the need for still more gear restrictions and prohibitions, stricter quotas, more seasonal and area closures, and stricter size and trip limits. If political considerations diminish the effectiveness of open-access regulations to achieve even short-term biological goals, then the need for additional regulation arises more quickly. Fishermen tend to perceive the continued introduction of new, more restrictive, costly, and complex regulations as a source of instability in the fishery and to see the management agency as part of or the source of the problem[5]. The likely outcomes of traditional methods of management are higher fishing costs, less productive fishermen, additional regulations to control fishing effort in the long term, and an adversarial relationship between fishermen and fishery managers.

Methods of Restricting Access to a Fishery

Regulations that restrict access to a fishery are classified as limited-entry methods of management. They attempt to overcome the fundamental economic incentives to overfish by establishing new systems of fishing rights or privileges in terms of a limited right of access or a limited right to take specific quantities of fish.

This paper focuses on the two most common forms of limited entry: License limitation and catch rights. Various existing programs that use license limitation or catch rights are discussed in Clark et al. (1988), Geen and Nayar (1988), Huppert (1987), Mollett (1986), Pearse (1979), Rettig and Ginter (1978), Rettig (1984) and Townsend (1990). Other less frequently mentioned alternatives include territorial use rights (Christy, 1982; Smith and Panayotou, 1984) and sole ownership (Keen, 1988; Scott, 1955). Licenses represent the right to participate in the fishery at any level of activity. Catch rights (also called individual transferable quotas, ITQ's, or individual fishermen's quotas, IFQ's) represent the right to land specific quantities of fish. Territorial use rights represent the exclusive right to harvest from a given area, and have been commonly associated with relatively sedentary species; private oyster leases are a good example. Sole ownership in large bodies of water appears to be of interest primarily as the theoretical standard with which the various institutional arrangements for harvesting fishery resources are compared. Keen (1988), however, recently advocated sole ownership as a management tool.

License Limitation

License limitation is a management system in which the right to deploy some basic unit of effort, usually the vessel, is restricted to those with licenses, and the number of licenses is limited by the regulating agency[6]. License limitation

[4] Fishery rent refers to the overall sum for all fishermen of profits, including a return to capital, above opportunity costs for labor. Over time, the existence of profits above opportunity costs would attract new effort into the fishery unless the capital costs of entry were prohibitively high. If relatively large amounts of effort entered the fishery whenever fishery rent existed, then the resulting external costs would wipe out most or all of the difference between profits and opportunity cost. If relatively small amounts of effort entered the fishery, then some fishery rent would remain and would accrue to fishermen as additional profit.

[5] I thank Dean Ahrenholz and John Gauvin for pointing this out to me.

[6] Minimum income requirements, which reserve the commercial allocation of a fish stock for those who derive at least x % of their earned income from commercial fishing, possess some attributes of the license limitation method of restricting access to a fishery in that individuals must qualify to participate in the fishery and that catch per individual would be unrestricted until the commercial quota had been achieved. However, minimum income requirements differ from license limitation in that 1) individuals must qualify each year rather than only at the beginning of a limited-entry program, 2) there would not be a limit on the total number of potential qualifiers, and 3) qualifiers could not sell or rent their fishing privileges to potentially more profitable individuals. It is transferability of fishing privileges that enables a given quantity to be harvested at minimum cost. Hence, from an economic efficiency perspective, minimum income requirements may or may not result in the lowest possible costs of producing a given quantity of fish. Also, items 1) and 2) imply that minimum income requirements would not restrict the potential long-term growth in fishing effort by persons who may qualify as full-time commercial fishermen or the long-term growth in effort by recreational fishermen (for whom minimum income requirements do not apply). The primary effect of minimum income requirements is to protect the competitive position of full-time commercial fishermen by preventing part-time commercial and recreational fishermen from selling their catches.

was the first method used to restrict access to a fishery, probably because the concept of a license was familiar to fishery managers and fishermen, because most limited-entry programs began with an agreement that there were or would soon be too many fishermen, and because the license system was relatively easy to administer and enforce (Rettig, 1984). The following discussion summarizes more detailed descriptions found in Beddington and Rettig (1984), Crutchfield (1979), Huppert (1987), Pearse (1980), Rettig (1984), Townsend (1990), and Wilen (1988).

Economic Effects

License limitation is an attempt to fix fishing mortality by limiting the number of vessels in the fishery. In theory, potentially large conservation benefits are possible when fishing mortality can be fixed, usually at a reduced level when compared to the status quo. Another advantage of a fixed fishing mortality is that fishery managers would not have to predict changes in stock abundance. Catches would increase automatically when the size of the fish population is above average and would decrease automatically when the fish population is below average. In addition, license limitation would offer a means of inducing compliance with other regulations in the fishery because illegal behavior could result in loss of license.

In practice, fishing mortality and fishing effort are seldom equivalent. Effort is produced by a variety of factors such as vessel size, engine type and horsepower, the number and type of gear, the number of crew, and fishing time. Limitations on the number of vessels would encourage fishermen to increase their fishing power through improvements in other, unrestricted components of effort (Rettig, 1984). This phenomenon has been called "capital stuffing." For example, new, larger vessels could replace old, smaller vessels. And all vessels could add more sophisticated fish finders, more and newer gear, larger crews, more and/or longer trips. Although most license limitation programs restrict other components of effort, such as vessel tonnage, as well as the number of vessels, it is impossible to control all aspects of fishing effort, even if fishing technology appears to be fairly inflexible. The effect of license limitation would be similar to that for gear restrictions in that those with licenses would increase their use of unrestricted components of effort. The two management systems differ in that there could be no net increase in the number of operating units with license limitation.

Licenses acquire value by excluding nonlicense holders from participating in the fishery. Licenses acquire a value approximately equal to the expected profitability of adding another vessel to the fishery. If licenses expired and were reissued every year, then the license value would represent the expected profits for the current fishing year. If licenses never expired, then the license value would reflect the net present value of expected current and future profits. Licenses issued in perpetuity would be preferred as a means of ensuring a stable economic environment for employment and investment.

License values represent the creation of wealth. This wealth is derived from the fishery rent that would normally have been dissipated via the external costs created by extra fishing effort that would have been expended in an open-access fishery. Fishermen would receive a windfall of new wealth if licenses were distributed initially by random drawing (lottery) or given away according to a criterion usually based on some measure of historical participation and investment in the fishery[7]. Theory and experience suggest that even with a moratorium to prevent entry into the fishery during the planning phase, fishing effort would increase as existing fishermen compete to qualify for licenses. The increase in fishing effort would be more pronounced without a moratorium as new entrants scramble to qualify for licenses and wealth. Once licenses have been distributed, fishermen would gain or lose wealth over time as the value of their licenses fluctuated due to changes in the factors (e.g., prices, costs, catch rates, and interest rates) that determine current and expected future profits in the fishery. The creation of new wealth makes it imperative that fishery managers and fishermen cooperate during the formulation of the licensing system.

The transferability of licenses is a desirable characteristic. Transferability facilitates the development of a market in which licenses are traded or leased[8]. An organized market for licenses would allow new fishermen to enter the fishery. License limitation would not bar new entrants, but they would have to buy a license and someone else would have to leave the fishery. The market for licenses would encourage the least profitable fishermen to leave the fishery if offers for their licenses were greater than what they expected to earn in the fishery, but at least they would be paid to leave.

The existence of a market value for licenses implies that those who fish would incur an additional fixed cost equal to the value of the license. If the license were leased, then there would be a (cash) rental fee. If the license were owned by the fisherman, then there would be an opportunity cost in that the fisherman could retire and rent or sell the license to another. In essence, the fisherman would have to pay himself for the use of the license. This opportunity cost would prevent license holders from becoming complacent and inefficient because if they were, they would be able to earn more by selling or renting the license to others. Competition in the market for licenses

[7] In theory, licenses could also be distributed by auction but the Magnuson Fishery Conservation and Management Act does not allow permits or licenses to be issued for amounts in excess of the administrative cost of issuing the licenses. The government would receive the wealth generated through the initial distribution of licenses if they were auctioned. Newly created wealth could be shared by fishermen and the government if annual fees were established as a means of financing the costs of research, administration, and enforcement of fishery management plans, and the purchase and retirement (buy-back) of licenses as a means of reducing participation in the fishery.

[8] Licenses would be valuable in terms of their ability to generate profits even if they were not officially transferable. If licenses were assigned to fishing vessels (to prevent nonfishermen from owning licenses), then license value would be incorporated into the price of the vessel so that the purchase of the right to fish would require the additional purchase of a particular vessel. If licenses were assigned to individuals rather than to vessels, then fishermen who would have sold their licenses were they transferable would be expected to enter into off-the-record partnerships with other potentially more profitable fishermen. License holders would be reluctant to retire from the fishery because their income from the license would simply vanish.

ensures that those most willing or able to buy or lease licenses, usually the most efficient and profitable fishermen, would acquire or lease them, whatever the initial distribution.

Also, the market for licenses would enable the government to reduce fishing effort by buying and retiring licenses. However, buy-back schemes generally have been found to be expensive[9]. Usually, a large number of licenses must be purchased to reduce the overall catch by enough to rebuild depleted fish stocks.

Other Considerations

License limitation programs suffer from shortcomings in addition to the problem of capital stuffing. For one thing, if the market price of licenses were determined by fishermen who work full time in the restricted fishery, then license limitation would tend to exclude fishermen who participate in other fisheries at one time or another during the year. The problem is that those who wish to participate in a restricted fishery on a limited basis may not earn enough in it to justify the purchase of a license.

Other details would have to be addressed before an acceptable and workable licensing system could be established. For example, would the use and transfer of licenses be restricted within particular vessel size classes, gear types, seasons, or geographical areas to maintain historical patterns of participation by various interest groups or to reduce the number of competitors within each group (see Wilen, 1988; Dupont, 1990)? Would ownership of licenses be restricted to fishermen, or could nonfishermen such as dealers, processors, recreational fishing clubs, nonfishing corporations, and environmental groups own licenses? Could license limitation be enforced if licenses were not required in state waters?

Catch Rights

Catch rights represent a management system in which fishermen would receive transferable certificates, with each certificate conferring the right to catch and sell a small, fixed proportion of the total allowable catch. The total allowable catch would be determined each year by the management council. An alternative formulation would define each certificate as the right to catch a relatively small, fixed amount of fish. In either case, each fisherman's quota could consist of a few or many certificates to accommodate differences in scales of operation. Annual revisions of the estimated total allowable catch (TAC) would offer direct control over each season's total catch. If certificates were expressed as a fixed percentage of the TAC, then each fisherman's quota would be automatically revised whenever a new TAC was announced. If certificates were expressed in pounds, then the government could either issue additional certificates whenever TAC was increased or buy certificates whenever TAC was reduced[10]. More detailed discussions are found in Clark and Duncan (1986), Clark et al. (1988), Copes (1986), Crutchfield (1979), Geen and Nayar (1988), Moloney and Pearse (1979), Peacock and MacFarlane (1986), Pearse (1980), and Robinson (1986).

The use of catch rights as a management system is similar to license limitation in that both systems would create marketable fishing rights or privileges. License limitation would confer the right to deploy fishing effort, but each fisherman's catch would be unrestricted. This would lead to capital stuffing as fishermen compete to maintain or increase their shares of the overall catch. Catch rights would represent a more complete system of fishing rights: The right to deploy effort and catch a particular quantity of fish. Catch rights would restrict access to the fishery only in that fishermen without certificates could not fish. But catch rights would not reduce the number of participants to a predetermined level as with license limitation. The fishery could have any number of fishermen with small, medium, or large vessels, provided that they own or lease certificates. Nevertheless, the number of active participants in the fishery would be expected to decline because the total allowable catch (summed over all catch rights) would be less than what would be caught without catch rights as a means of rebuilding depleted fish stocks.

Economic Effects

Catch rights would offer advantages to fishermen by enabling them to plan investment and harvesting strategies more efficiently. Catch rights would eliminate much of the uncertainty about the magnitude of each fisherman's catch[11]. In essence, a known portion of the fish stock would be reserved for each fisherman with catch rights. Therefore, fishermen would not be compelled to invest in extra fishing power (capital stuffing) to compete for fish on a first-come-first-served basis. They could invest in the fishing power required to minimize rather than maximize the cost of harvesting a given quantity of fish. In addition, with transferable catch rights of relatively small denominations, the investment in catch rights would not necessarily be prohibitive for fishermen with small vessels, part-time fishermen, and fishermen who participate in several fisheries throughout the year. Another advantage is that the harvesting season could last longer with catch rights, thereby avoiding temporary market gluts which could reduce fish prices and quality. For example, fishing seasons could last longer because fishermen would be less likely to fish in poor weather, or they could postpone part of their catches to take advantage of higher prices later in the season. Nevertheless, most fishing would probably still occur when fish are most abundant to minimize the costs of locating and catching fish.

But what is to prevent fishermen from making additional trips and illegally landing fish in excess of their quotas? Catch rights will not work unless each fisher-

[9] The inability to distribute licenses by auction would eliminate a potentially large source of revenues with which to fund a buy-back program.

[10] The inability to auction or sell catch rights for more than the cost of issuing them would limit the ability of the government to generate the revenues required to buy catch rights whenever the TAC was reduced. Therefore, in practice, it may be preferable to define catch rights as a percentage of TAC. This would eliminate the need for a large budget to reduce the number of outstanding catch rights, but it would add another element of uncertainty about the magnitude of each fisherman's catch.

[11] Some uncertainty about future catches would remain because the management agency could adjust the number of certificates outstanding (if certificates were expressed in pounds) or the number of pounds per certificate (if expressed as a percentage of total allowable catch) in response to annual variability in stock size.

man's quota of fish is really there when he wants it. Therefore, the government must enforce the rules so that fishermen have a reasonable expectation of being caught and convicted if they attempt to land more than their quotas. And there must be a relatively severe schedule of penalties for cheating, such as loss of catch, fines, and temporary or permanent revocation of fishing privileges. If enough fishermen are known to cheat, then others would be compelled to cheat also or else risk losing their shares of the overall catch. Dealers who buy illegally landed fish would also be subject to penalties. If government cannot enforce the rules, then the system has no chance of success. The implication is that substantial enforcement costs may be required to achieve adequate compliance.

Enforcement could be accomplished at dockside and could be costly because many individual quotas landed at many different ports would have to be monitored. Fishermen could underreport landings by failing to report the correct quantities, by landing fish surreptitiously at secret or existing landing sites, or by incorrect identification of species. Regulated red snappers might be reported as unregulated vermilion snappers, for example. Enforcement becomes more difficult as the numbers of fishermen, landing sites, and regulated species increases (Copes, 1986).

The Mid-Atlantic Fishery Management Council facilitated dockside enforcement for surf clams and ocean quahogs by issuing cage tags each year to fishermen in proportion to their individual quotas (U.S. Department of Commerce, 1990). Tags must be affixed to cages of surf clams and ocean quahogs before the cages leave the vessel and must be removed when cages are emptied at the final processing site. Anyone in possession of filled cages without a tag or empty cages with a tag is in violation of the management plan. Fishermen, dealers, and processors must report (among other things) tag numbers of cages that they handled. New Zealand implemented a double-entry data collection system to supplement dockside enforcement in its restricted-access fisheries (Muse and Schelle, 1988). Both the fisherman and buyer must file separate records of each off-loading. Computer analysts then check to determine that the records match and that each fisherman's quota has not been exceeded.

If government demonstrates that it can successfully enforce the rules, then fishermen will recognize that catch rights truly represent a limit on the ability to land and sell fish. More important, fishermen will then be willing to pay for catch rights to expand their scales of operation, to enter the fishery, or to adjust their holdings of catch rights to match their actual annual catches. The value per catch right would be determined in the market for catch rights by the capitalized value of additional profits expected to be earned over time with an extra certificate. Events, such as a higher ex-vessel price, that would increase the profitability of fishing would cause an increase in the price per certificate. Conversely, such events as an increase in fuel prices which would decrease the profitability of fishing, would cause a decrease in the price per certificate. Fishermen would incur an additional variable cost equal to the market value of their catch rights if they leased catch rights or an opportunity cost if they owned catch rights. Fishery rent would accrue to owners of catch rights rather than be dissipated among a larger number of fishermen as in an open-access fishery.

An adequate level of enforcement would create incentives for fishermen to conserve fish for the future and to report others who are known to violate the rules. Once fishermen have a substantial investment in catch rights, then it becomes to their advantage to protect their investments by voluntarily reporting those who attempt to cheat[12]. Widespread cheating would reduce, and eventually eliminate, the market value of catch rights: Fishermen would not be willing to pay for something that they could obtain for free simply by cheating with impunity (Peacock and MacFarlane, 1986).

When a system of catch rights is initiated, a formula would have to be established to determine who would be included in the program and how many certificates each person would receive. The initial allocation of catch rights must be considered by fishermen to be equitable. The opportunity for the initial recipients of catch rights to gain a windfall of wealth suggests that negotiations about criteria to qualify for an initial distribution of catch rights probably will be arduous and contentious. Certificates could be distributed initially in a variety of ways. Most likely they would be given away based on criteria such as each fisherman's historical landings, investment, or experience in the fishery over some recent period[13]. As with license limitation, fishing effort would increase during the planning stages as fishermen compete to qualify for an initial distribution of catch rights. Catch rights could be issued seasonally, annually, in perpetuity, or any other convenient term. Longer terms would lower the costs of administration and provide more stability for investment (in vessel, gear, and career choice) purposes.

As a means of rebuilding the fish population, each fisherman would probably receive certificates to catch fewer fish than he historically had caught. Transferability of certificates would allow a market to develop in which certificates would be redistributed to better match desired levels of production. The most profitable fishermen would increase their quotas by buying or leasing catch rights from the least profitable fishermen, who would then probably switch to other fisheries. By selling their catch rights, fishermen who leave the fishery would at least receive some financial compensation for leaving. From an economic perspective, the redistribution of catch rights to the most profitable fishermen would

[12] In contrast, open-access regulatory methods generally do not foster self-enforcement for economic reasons, although a majority of fishermen may comply for moral reasons. With open-access regulations, the temptation to cheat would always exist except for the penalties that could be levied if a fisherman were caught and convicted in violation of the rules. Severe penalties and/or a high probability of detection and conviction may prevent fishermen from cheating. Relatively small penalties and a low probability of detection and conviction would encourage fishermen to cheat. And individuals have no incentive to voluntarily obey the rules if others are known to violate them with impunity because fish conserved by one fisherman would likely be harvested by another. The alternative to continuous enforcement would be widespread cheating, which would thwart the intent of the regulations.

[13] Catch rights could also be auctioned, but the Magnuson Act currently does not permit fees in excess of administrative costs.

improve economic efficiency; fish would be landed at minimum cost. However, it could also lead to additional inefficiencies in other fisheries if access to them is not controlled.

Transferable catch rights offer additional consequences. First, transferability gives fishermen the flexibility to match their holdings of catch rights to their desired scales of operation, which may vary due to differences in boat size or a desire to participate in other fisheries during the year. Second, without transferability, fishermen would be unlikely to match exactly annual catches with their holdings of catch rights. Fishermen could end the season with unused catch rights. Or, fish would be discarded if actual catches exceeded holdings of catch rights. Third, transferable catch rights facilitate entry into a fishery with controlled access. Fishermen could enter the fishery at a low level with a relatively small initial investment in catch rights. Then they could gradually increase their holdings of catch rights as they gain experience in the fishery and their financial position improves. Fourth, in addition to fishermen, other people associated with the fishery may wish to participate in the market for catch rights. For example, dealers and processors may wish to purchase catch rights to ensure an adequate and timely supply of fish. Vessels could be hired and dispatched to the fishing grounds as needed to fill sales orders, processing, and storage capacity.

Other Considerations

Multispecies fisheries present obstacles for the successful use of catch rights. Total allowable catches would need to be specified and catch rights would need to be issued in one form or another for all major species or species groups in the fishery. Catch rights issued for fish in general, regardless of species, may not offer adequate protection for severely depleted species. On the other hand, catch rights issued for each species would cause problems for fishermen who need to match their multispecies catches to many quotas and would increase monitoring and enforcement costs. An appropriate compromise may be to issue catch rights for species groups which are generally caught together and which exhibit similar biological characteristics.

In addition, the potential exists for an increased volume of discarded fish. Catch rights could lead to "high-grading" in which fishermen sort and discard the lowest valued fish so as not to exceed their individual quotas for a given species. Also, after their individual quotas for one species or species group has been reached, fishermen could continue to fish for other species and discard their additional catches of the species for which quotas had already been filled. The practice of discarding makes the choice of appropriate total allowable catches, which must account for total extractions (discards plus landings) from the wild fish populations, more difficult. Copes (1986) offers a more detailed discussion of the potential problems with catch rights as a management technique.

Summary and Discussion

Traditional, open-access methods of regulation in a fishery will not significantly improve the economic performance of fishermen. In the short term, fishermen will be forced to use less productive and/or more costly methods of production. In the long term, the potential biological and economic benefits of regulation will not be sustained because access to the fishery would remain unrestricted. Temporary biological improvements in fishery resources will encourage new fishermen to enter the fishery and existing fishermen to increase their effort. Even if traditional regulations proved ineffective and biological improvements were not forthcoming, fishing effort could increase over time due to cost-saving technological change and increases in the demand for commercial fishery products and recreational fishing activities. Increases in fishing effort will tend to minimize potential long-term economic and biological benefits of regulation. New regulations will have to be implemented to further reduce fishing mortality by closing loopholes, restricting other gears or components of effort, or prohibiting new innovations. The result of management with unrestricted access to the fishery will be additional and more costly and complex regulations as competition increases for dwindling fishery resources.

Limited-entry systems of management would restrict access to a fishery through the issuance of a limited number of fishing rights or privileges. These fishing rights would acquire a value which would accrue to their owners as an additional benefit from fishing. The market price of fishing rights would also increase the cost of participation in a fishery as an incentive for the least efficient fishermen to shift to other fisheries or land-based employment opportunities. This would likely improve economic performance in the restricted fishery, but it could also lead to additional inefficiencies in other fisheries if access to them is not controlled. Greater regulation in alternative fisheries may be necessary if the additional fishing effort leads to overfishing of the alternative species or hastened their decline if they were already overfished.

License limitation and catch rights are the most common methods of restricting access to a fishery. With license limitation, qualifying fishermen would receive a license for the right to fish, but each fisherman's allowable catch would be unrestricted. Among other things, Townsend (1990) concluded that license limitation slows the race for fish on a first-come-first-served basis only in that there would be fewer fishermen. Hence, license limitation does not contribute to biological conservation of fish stocks. The quotas often accompanying limited entry offer biological conservation while license limitation offers economic benefits by reducing short-term crowding externalities.

Catch rights, when adequately enforced, have the potential to change fishing strategies. Ideally, catch rights should have certain desirable characteristics to facilitate attainment of economic efficiency and biological conservation. The catch right must be recognized by the judicial system as a legitimate and exclusive right of participation in the fishery, and it should be permanent so that fishermen individually and collectively believe that they have a vested interest in the continued well-being of the fishery resource. In addition, government must demonstrate that it can prevent fishermen from illegally landing fish in excess of their quotas. If these conditions are satisfied, then fishermen will have an

incentive to cooperate in the use of conservative harvesting strategies, including peer pressure to discourage noncompliance with fishery regulations and/or acceptable fishing practices (Scott, 1988). In this sense, the existence of catch rights would facilitate individual control over fishing effort as a substitute for some, but not necessarily all, direct government restrictions on fishing times, locations, gear types, and keep rates. Fishing effort would be limited, but fishermen would retain more flexibility in their choices of when, where, and how to fish, including the ability to fully utilize existing capital before replacing it. Catch rights could be complemented with traditional methods of regulation in specific circumstances. For example, minimum size limits could reduce catches of juvenile fish, and seasonal and area closures could reduce catches of spawning fish. However, the retention of open-access methods of regulation would also retain their negative qualities, with perhaps only the scale of their problems changed. It would be better to eliminate or simplify as many traditional regulations as possible rather than to add catch rights to a host of existing open-access regulations.

Why are traditional methods of regulation adopted if they are ineffective in the long term? For one thing, they offer at least temporary biological protection. Also, these types of regulations, especially gear restrictions and minimum income requirements, have tended to benefit politically dominant groups of fishermen by allocating a relatively larger share of the overall catch to their members (Karpoff, 1987). In this sense, traditional regulations minimize social and political discord due to regulation and hence may elicit relatively high voluntary compliance and may be relatively inexpensive to enforce.

Open-access regulations may be preferred over limited entry for philosophical reasons in what Acheson (1980) called the "Adam Smith response." The number of fishermen in a fishery is self regulated by competition. Limited entry may be perceived as an additional restraint on the free enterprise system in which a select few would be protected from normal competitive forces.

Economists counter with two arguments. First, because fish are common property, the unregulated free enterprise system does not result in optimal levels of fishing effort and overall harvest from the perspective of society as a whole. As Hardin (1968) wrote, "Freedom in a commons brings ruin to all." Open-access regulations allow as much freedom of access as possible while restricting how, when, and where people fish. Limited-entry regulations restrict access while allowing as much freedom as possible to choose how, when, and where to fish. Many fishermen and fishery managers may simply prefer to maintain the historical tradition of open access to marine fisheries. Second, limited entry would not protect individuals from competition for the limited number of fishing privileges as long as licenses or catch rights are transferable.

The prospect of a market-based distribution of fishing privileges may evoke additional opinions about limited entry. Many fishermen and fishery managers may oppose the potential redistributional effects of limited entry (Acheson, 1980). Open-access regulations allocate fish among fishermen on a first-come-first-served basis subject to certain restrictions described by the regulations. With limited entry, on the other hand, after the initial distribution of fishing rights, access to the fishery would be determined by market forces. Newcomers could buy or rent fishing rights to enter the fishery, and retirees would be paid to leave. But the final distribution of fishing rights among small-scale fishermen, large-scale fishermen, processors, and other investors would be different from open access and may be viewed as less predictable or less desirable than that of traditional regulations. Some fishermen may fear that they would receive an unfair initial distribution of fishing rights, that they may be excluded from the fishery altogether, or that ownership of fishing privileges would soon be purchased by wealthier fishermen and corporations. And excess capital and labor may not be easily transferred to other fisheries or land-based employment, which would create large short-term losses for those who were excluded.

Fishery managers may prefer open-access regulations if there is a large recreational fishery for which access cannot be easily controlled. Limited-entry programs are generally applied to commercial fisheries and traditional methods of regulation (e.g., bag limits and annual quotas) to the recreational sector. But without geographical separation of the fish stocks sought by commercial and recreational fishermen, open-access competition by the recreational sector would undermine the potential benefits of limited entry for the commercial sector.

It is not clear how limited entry could be applied to recreational fishermen. One option would be a separate limited-entry system of licenses or catch rights for recreational fishermen. A management system based on catch rights could include recreational fishermen more easily than could a system based on license limitation. Recreational fishermen could receive initial allocations of catch rights, probably by lottery because historical levels of participation in the fishery are difficult to verify. Then they could participate in the market for catch rights to increase or decrease their holdings of catch rights. Fishing tackle shops and marinas may wish to purchase catch rights for resale to recreational fishermen while charter and party boat operators may purchase catch rights for their clients. If recreational and commercial fishermen competed in the same market for catch rights, then the allocation of the total allowable catch between the recreational and commercial sectors would be determined in the market for catch rights rather than by tradition or political clout. By definition, fish would be allocated to their most highly valued uses because catch rights would be purchased by those most willing and able to pay for them. Nevertheless, if compliance is poor then enforcement would be costly because of the large numbers of fishermen and points of landing. Whatever methods are chosen, however, if recreational fishing effort is not restricted, then the potential biological and economic benefits of reducing commercial fishing effort would be minimized by long-term increases in recreational effort.

Finally, fishery managers and fishermen may hesitate to forego familiar open-access methods of management if they sense that economists, in their zeal, have

overstated the potential advantages of restricting access to a fishery and overlooked some of the disadvantages. In fact, early advocates of license limitation underestimated the ability of fishermen to expand their use of uncontrolled components of effort. Various license limitation programs have existed for many years and their advantages and shortcomings are now well documented (Townsend, 1990). In theory, the use of catch rights is superior to license limitation. However, management programs with catch rights are relatively new, and hence their effects in practice have not been as thoroughly scrutinized. Copes (1986) provides a discussion of potential problems in the implementation of catch rights.

Turvey (1964) noted that "(A) fishery is one of those spheres of economic policy where what is the best thing to do depends on what can be done." Nevertheless, given the long-term disadvantages of traditional, open-access methods of managing marine fisheries, it makes sense to explore the possibilities of alternative methods of regulating fishing effort. An empirical question is whether or not the potential benefits would exceed the costs of starting, monitoring, and enforcing a limited-entry system of management.

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Pacific Salmon, *Oncorhynchus* spp., and the Definition of "Species" Under the Endangered Species Act

ROBIN S. WAPLES

Introduction

In conjunction with a review of the biological status of Pacific salmon,[1] *Oncorhynchus* spp., initiated in 1978 by the National Marine Fisheries Service (NMFS) and the U.S. Fish and Wildlife Service (FWS), three policy position papers were drafted for the consideration of Columbia River salmon under the Endangered Species Act (ESA or "the Act"). The draft papers were intended to provide guidance at three critical stages in ESA evaluations: Determination of what constitutes a "species" under the Act (and what, therefore, may merit protection), determination of thresholds for listing as threatened or endangered, and

[1] The term "Pacific salmon" has traditionally referred to species of the genus *Oncorhynchus*, five of which (*O. gorbuscha*, *O. keta*, *O. kisutch*, *O. nerka*, and *O. tshawytscha*) occur in North America. The recent decision to move the western trouts from the genus *Salmo* to *Oncorhynchus* calls this usage into question. In this document, "Pacific salmon" is used to include anadromous forms of *O. clarki* and *O. mykiss*, as well as the five above mentioned species.

Robin S. Waples is with the Coastal Zone and Estuarine Studies Division, Northwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.

ABSTRACT—For purposes of the Endangered Species Act (ESA), a "species" is defined to include "any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature." Federal agencies charged with carrying out the provisions of the ESA have struggled for over a decade to develop a consistent approach for interpreting the term "distinct population segment." This paper outlines such an approach and explains in some detail how it can be applied to ESA evaluations of anadromous Pacific salmonids.

The following definition is proposed: A population (or group of populations) will be considered "distinct" (and hence a "species") for purposes of the ESA if it represents an evolutionarily significant unit (ESU) of the biological species. A population must satisfy two criteria to be considered an ESU:

1) It must be substantially reproductively isolated from other conspecific population units, and

2) It must represent an important component in the evolutionary legacy of the species.

Isolation does not have to be absolute, but it must be strong enough to permit evolutionarily important differences to accrue in different population units. The second criterion would be met if the population contributes substantially to the ecological/genetic diversity of the species as a whole.

Insights into the extent of reproductive isolation can be provided by movements of tagged fish, natural recolonization rates observed in other populations, measurements of genetic differences between populations, and evaluations of the efficacy of natural barriers. Each of these methods has its limitations. Identification of physical barriers to genetic exchange can help define the geographic extent of distinct populations, but reliance on physical features alone can be misleading in the absence of supporting biological information. Physical tags provide information about the movements of individual fish but not the genetic consequences of migration. Furthermore, measurements of current straying or recolonization rates provide no direct information about the magnitude or consistency of such rates in the past. In this respect, data from protein electrophoresis or DNA analyses can be very useful because they reflect levels of gene flow that have occurred over evolutionary time scales. The best strategy is to use all available lines of evidence for or against reproductive isolation, recognizing the limitations of each and taking advantage of the often complementary nature of the different types of information.

If available evidence indicates significant reproductive isolation, the next step is to determine whether the population in question is of substantial ecological/genetic importance to the species as a whole. In other words, if the population became extinct, would this event represent a significant loss to the ecological/genetic diversity of the species? In making this determination, the following questions are relevant:

1) Is the population genetically distinct from other conspecific populations?

2) Does the population occupy unusual or distinctive habitat?

3) Does the population show evidence of unusual or distinctive adaptation to its environment?

Several types of information are useful in addressing these questions. Again, the strengths and limitations of each should be kept in mind in making the evaluation. Phenotypic/life-history traits such as size, fecundity, and age and time of spawning may reflect local adaptations of evolutionary importance, but interpretation of these traits is complicated by their sensitivity to environmental conditions. Data from protein electrophoresis or DNA analyses provide valuable insight into the process of genetic differentiation among populations but little direct information regarding the extent of adaptive genetic differences. Habitat differences suggest the possibility for local adaptations but do not prove that such adaptations exist.

The framework suggested here provides a focal point for accomplishing the major goal of the Act—to conserve the genetic diversity of species and the ecosystems they inhabit. At the same time, it allows discretion in the listing of populations by requiring that they represent units of real evolutionary significance to the species. Further, this framework provides a means of addressing several issues of particular concern for Pacific salmon, including anadromous/nonanadromous population segments, differences in run-timing, groups of populations, introduced populations, and the role of hatchery fish.

consideration of the possible role of artificial propagation in recovery plans for listed "species."

On receipt of petitions (April-June 1990) to list several populations of Pacific salmon as threatened or endangered "species" under the Act, NMFS sought public comments on draft Policy Position Paper #1, "Definition of Species" (a summary of a longer document by Utter (1981)). Based on that paper and public comments on it, discussions of the issue by the ESA Technical Committee, and ideas discussed at a Vertebrate Population Workshop convened in June 1990 by FWS and NMFS, Waples (1991a) prepared a NOAA Technical Memorandum that formed the basis for NMFS' "Interim Policy on Applying the Definition of Species Under the Endangered Species Act to Pacific Salmon" (56 FR 10542; March 13, 1991). After considering public comments on the Interim Policy and the supporting NOAA Technical Memorandum, NMFS published a Final Policy on this issue (56FR 58612; Nov. 20, 1991). Those comments were also considered in preparation of this paper.

Background of the Endangered Species Act

The stated purposes of the Endangered Species Act of 1973, as amended (16 U.S.C. 1531 et seq) are to "provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved, [and] to provide a program for the conservation of such endangered species and threatened species." "Species" is used in a more expansive way in the ESA than biologists or taxonomists generally use the term. In the original (1973) version of the Act, a "species" was defined to include "any subspecies of fish or wildlife or plants and any other group of fish or wildlife of the same species or smaller taxa in common spatial arrangement that interbreed when mature." Use of this language established that the scope of the Act extends beyond the traditional biological definition of species to include smaller biological units. Amendments in 1978 (Public Law 95-632 (1978), 92 Stat. 3751) provided the current language in the Act: A "species" is defined to include "any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature." Unfortunately, although the Act thus allows listing of populations that are "distinct," it does not explain how population distinctness shall be evaluated or measured.

Nevertheless, there is some guidance relevant to this issue. A review of legislative history indicates that an important motivating factor behind the Act was the desire to preserve genetic variability, both within and between species. For example, the House of Representatives described the rationale for House Resolution 37, a forerunner to the Act, in the following terms (H.R. Rep. 412, 93d Cong., 1st Sess., 1973):

"From the most narrow possible point of view, it is in the best interests of mankind to minimize the losses of genetic variations. The reason is simple: They are potential resources. They are keys to puzzles which we cannot yet solve, and may provide answers to questions which we have not yet learned to ask."

On the other hand, in 1979 the General Accounting Office (GAO)[2] recommended that the authority to list vertebrate populations under the ESA be removed. Although this recommendation was not adopted, the Senate Report to the 1979 amendments stated that "the committee is aware of the great potential for abuse of this authority and expects the FWS to use the ability to list populations sparingly and only when biological evidence indicates that such action is warranted" (Sen. Rep. 151, 96th Cong., 1st Sess., 1979). Finally, the ESA (Sec. 4(b)(1)(A)) specifies that listing decisions should be based "solely on the basis of the best scientific and commercial data available."

Although not entirely self-contradictory, the charge to conserve irreplaceable genetic resources but to do so sparingly (and scientifically) clearly establishes a certain tension in the process of "species" determination for vertebrate populations under the ESA. The approach adopted here is an attempt to balance these themes in a framework consistent with both the letter and intent of the ESA.

Definition: A vertebrate population will be considered distinct (and hence a "species") for purposes of conservation under the Act if the population represents an evolutionarily significant unit[3] (ESU) of the biological species. An ESU is a population (or group of populations) that:

1) Is substantially reproductively isolated from other conspecific population units, and

2) Represents an important component in the evolutionary legacy of the species.

Note that the dual criteria reflect two common meanings of "distinct": The criterion of reproductive isolation emphasizes the concept of "separate" or "apart from," whereas the criterion of evolutionary importance focuses on characteristics that are "different" or "unique."

Isolation does not have to be absolute, but it must be strong enough to allow evolutionarily important differences to accrue in different population units. Population characteristics that are important in an evolutionary sense must have a genetic basis; therefore, the second criterion would be satisfied if the population in question contributes substantially to the overall genetic diversity of the species. Because ecological diversity may foster local adaptations (and hence genetic diversity), a population that occupies unusual or distinctive habitat or in other ways represents an important ecological adaptation for the species may also be an ESU.

The term "evolutionary legacy" is used in the sense of "inheritance," i.e., something received from the past and carried forward into the future. This reflects

[2] GAO. 1979. Endangered species—a controversial issue needing resolution. Rep. to Congress, Gov. Account. Off., Wash., D.C.

[3] The term "evolutionarily significant unit" can be traced to Ryder (1986), who reported that the term was used at a 1985 meeting of zoo biologists and systematists in Philadelphia. The usefulness of this concept in the context of ESA evaluations was stressed at the Vertebrate Population Biology Workshop by A. Dizon (NMFS, Southwest Fisheries Science Center, La Jolla, Calif.). See Dizon et al. (In press) for additional discussion of this and related ideas with an orientation toward marine mammals.

the concern expressed in the Act (Sec. 2(a)(5)) for "better safeguarding, for the benefit of all citizens, the nation's heritage in fish, wildlife, and plants." Specifically, the evolutionary legacy of a species is the genetic variability that is a product of past evolutionary events and which represents the reservoir upon which future evolutionary potential depends. Conservation of these genetic resources helps to ensure that the dynamic process of evolution will not be unduly constrained in the future. Although the Act (Sec. 2(a)(3)) also notes that species "are of esthetic, ecological, recreational, and scientific value to the nation and its people," focussing on these attributes without regard to the underlying genetic basis for diversity is not a sound strategy for long-term species survival. Furthermore, societal values change rapidly on an evolutionary time scale, and "species" with no apparent significance today may be found to be "valuable" at some point in the future. It is better, then, to focus on conserving important genetic resources; if this is accomplished, then the other benefits of biodiversity (including various societal interests) follow naturally.

The framework adopted here provides a focal point for accomplishing the major goal of the Act—to conserve the genetic diversity of species and the ecosystems they inhabit. At the same time, it allows discretion in the listing of populations by requiring that they represent units of evolutionary significance to the biological species. In this framework, reproductive isolation is a necessary but not a sufficient condition for a population to be considered "distinct." Given enough time, an isolate may evolve into an ESU, but isolation by itself does not confer distinctness.

Application to Pacific Salmon

Application of the ESU concept to Pacific salmon requires consideration of reproductive isolation and ecological/genetic diversity. For convenience these concepts are considered separately here, but it is recognized that they are inherently related.

Reproductive Isolation

With Pacific salmon, reproductive isolation[4] is seldom a black-and-white situation; rather, it is a question of degree (e.g., Ricker, 1972). Although the homing instinct is well documented in these species, natural straying does occur (Quinn, 1984), and anadromous[5] spawning populations that are completely isolated from other conspecific populations are probably rare. A relevant question thus becomes: How much exchange with other populations can a salmon population experience and still be considered an ESU? Similarly, it is important to consider whether isolation is a recent phenomenon or whether it represents a long-standing condition.

One approach to this question emphasizes the effects of migration in inhibiting the process of genetic differentiation. The term "gene flow" is commonly used to describe the movement of genes from one population to another; that is, gene flow represents genetically effective migration. An oft-cited maxim based on the work of Sewall Wright (1978) is that gene flow between populations at the rate of one individual per generation is sufficient to prevent the tendency for different alleles to be fixed by chance (genetic drift) in different populations. Migration (the physical movement of individuals) may occur at a higher rate than gene flow if some migrating individuals have reduced reproductive success or fail to reproduce entirely.

Although gene flow at the level of one individual per generation may prevent extreme genetic divergence, it is not sufficient to equalize allele frequencies across populations, and Wright (1978) also pointed out that genetic differentiation is by no means negligible even if gene flow occurs at several times this rate. Furthermore, the above comments apply to a balance between migration and genetic drift of neutral alleles. Selection for locally adapted alleles can offset the homogenizing effects of gene flow. Thus, substantial differences among populations can be maintained at strongly selected loci, while frequencies at neutral loci remain relatively uniform (Slatkin, 1987).

Another way to consider the migration problem is to view it as a question of replacement. In this context, the relevant question is this: If all individuals in the population in question were permanently removed, would the area naturally be repopulated by individuals of the same biological species, and if so, within what time frame? Presumably, an area that would be naturally repopulated at or near the previous abundance level in a short time would be unlikely to harbor an ESU. This will be a largely theoretical exercise for populations being considered for protection under the Act. However, information for other populations and/or species may provide some insight into this process.

The level of migration or gene flow occurring among populations can be evaluated in several ways. Approaches that may prove useful for Pacific salmon include:

1) Use of tags to estimate straying rates;
2) Intentional genetic marking of populations;
3) Use of genetic indices (e.g., Wright's (1978) F_{ST} or Slatkin's (1985) private allele method) to estimate levels of gene flow;
4) Observations of recolonization rates; and
5) Identification of physical or geographic features likely to act as barriers to migration.

Since the 1950's, extensive data bases have been developed that provide important information about the oceanic distribution of Pacific salmon (Hartt, 1962).[6] More recently, physical tags have been used to study migrations of fish from individual populations (Johnson, 1990). However, tagging efforts typically focus on hatchery stocks, and much less is known about natural straying rates. Furthermore, tagging studies do not provide direct evidence of gene flow. A salmon

[4] This discussion of reproductive isolation focuses on the degree to which a population is isolated from genetic contact with other natural populations. Straying from hatchery stocks and intentional transfers of fish from one area to another are discussed in the section on "Special Considerations: Hatchery Fish."

[5] Nonanadromous populations or segments of populations are considered in the section on "Special Considerations: Anadromy/Nonanadromy."

[6] See also subsequent International North Pacific Fisheries Commission Bulletins on salmon distribution.

may swim into a nearby stream (and perhaps be counted as a stray) before ultimately making its way to its natal stream to spawn. Reproductive success of strays may also be less than that of fish from the local population.

A direct measurement of gene flow can be obtained by monitoring changes over time in the frequency of genetic markers characteristic of different populations. Because Pacific salmon populations are typically characterized by different frequencies of the same suite of alleles, rather than by qualitative differences in the types of alleles present (Utter et al., 1980, and many more recent references), it often will be difficult to measure gene flow precisely without enhancing the frequencies of different alleles in different populations (intentional genetic marking). Although the few genetic marking studies that have been conducted with Pacific salmon (Seeb et al., 1986; Lane et al., 1990) have provided important information, opportunities for such studies involving populations that are potential candidates for ESA listing are likely to be limited.

An indirect measurement of gene flow is provided by Wright's and Slatkin's methods, which measure some of the genetic consequences of migration. Accuracy of such estimates depends on the degree to which the various assumptions of the models used are satisfied. Notably, both methods assume selective neutrality of the alleles used, and results may be sensitive to the geographic configuration of the study sites included. Both methods are also based on equilibrium models and may overestimate migration rates if isolation has been too recent for a balance to develop between the forces of migration and genetic drift.

The presence of unique alleles (those found in only one population or one geographic region) may also provide insight into the degree of reproductive isolation. A major concern in evaluating such data is sampling error; that is, the failure to find the alleles in other localities may be due to inadequate sampling. Nevertheless, alleles that have been found in only one area and occur there at moderate or high frequency suggest a substantial degree of reproductive isolation. The occurrence of a number of unique alleles at lower frequency may also be indicative of reproductive isolation.

Opportunities to observe recolonization are not common with Pacific salmon, but they do occur. Aspinwall (1974) described one experiment that eradicated an entire run of pink salmon to study straying. Natural events (e.g., the eruption of Mount St. Helens) sporadically occur that cause extinction of populations or allow access to previously blocked habitat. In evaluating the results of such "experiments," it should be recognized that if intraspecific interactions (such as competition) are acting to hinder the success of migrants or strays, recolonization of empty habitat may occur at a higher rate than expected from migration rates among fully-seeded populations.

Because natural straying in Pacific salmon seems to be largely confined to nearby areas (Quinn and Fresh, 1984), geographic proximity of a population from other conspecific populations may provide a useful approximation of the degree of reproductive isolation. A number of studies of Pacific salmon have found genetic clustering of populations to occur largely along geographic lines (see references in Waples, 1991b). However, both types of exceptions to this pattern—pronounced differences between nearby populations and lack of differences between distant populations—have also been found, which emphasize the fact that distance is not the only barrier to gene flow. Consideration should also be given to other factors (e.g., geological history and physical and environmental gradients) that can affect population structuring. It must also be recognized that what appears to be a barrier to a biologist may not be a barrier to fish, and vice versa. Inferring barriers to migration on the basis of geographical or physical features alone can be misleading in the absence of supporting biological information.

As can be seen from this brief discussion, each of the above approaches has limitations. Nevertheless, it is important to consider all available information because the various approaches provide different insights into the question of reproductive isolation. Recolonization rates provide the most direct indication of the likelihood that a population, if eliminated, would become reestablished naturally. Approaches 1, 2, and 4 can provide data on current levels of migration or gene flow (over periods of one or a few generations). It is unlikely, however, that migration rates have been constant over long periods of time. In some cases, significant gene flow may occur only at intervals of decades or centuries. Genetic methods can be very informative in this context because they reflect the cumulative effects of gene flow over evolutionary time scales.

Ecological/Genetic Diversity

If available evidence indicates significant reproductive isolation, the next step is to determine whether the population in question is of substantial ecological/genetic importance to the species as a whole. In other words, if the population became extinct, would this event represent a significant loss to the ecological/genetic diversity of the species? In evaluating a population's contribution to ecological/genetic diversity, the following questions are relevant:

1) Is the population genetically distinct from other conspecific populations?
2) Does the population occupy unusual or distinctive habitat?
3) Does the population show evidence of unusual or distinctive adaptation to its environment?

Important factors to consider in addressing these questions include (but are not necessarily limited to) the following:

1) Genetic traits. Examples include presumably neutral characters detected by protein electrophoresis or DNA analyses as well as other genetically-based traits that are more difficult to quantify.
2) Phenotypic traits. Examples include morphological and meristic characters, occurrence of parasites, and disease and parasite resistance.
3) Life-history traits. Examples include time, size, and age at spawning; spawning behavior; fecundity; migration patterns; and timing of emergence and outmigration.
4) Habitat characteristics. This category includes such physical characteristics of the spawning and rearing habitat

as temperature, rainfall, stream flow, and water chemistry, as well as biological attributes of the local ecosystem. Location within a river drainage (e.g., upstream vs. downstream) and elevation can also be important in this regard. In a broader sense, the habitat for a population also includes areas encountered during the entire life cycle. Thus, a waterfall in the migratory route might select for robust fish capable of surmounting it, and a population with distinctive oceanic migration patterns probably utilizes marine habitat differently than do other populations.

Two points are important to consider in evaluating these types of data. First, such data can be properly evaluated only in relation to similar information for the species as a whole. That is, some reference data are necessary before one can determine that a particular population is distinct.

Second, it is unlikely that complete biological information will be available for any given ESA evaluation. This is particularly true for status reviews that must be conducted within a limited time period in response to formal petitions for listing. ESA determinations must be made on the basis of the best scientific information available at the time, and all relevant data should be considered.

Data from protein electrophoresis or DNA analyses permit direct inferences about genetic divergence and thus are particularly applicable to the question of population distinctness under the Act. However, if the common presumption is correct that the genetic characters detected by these methods are largely neutral with respect to natural selection, then it follows that differences among populations in these characters do not by themselves denote evolutionary significance, except in the sense that neutral genes may provide the raw material for future evolution. Rather, these genetic characters are primarily useful as indicators (or proxies) for evolutionary processes that can lead to local adaptation in other parts of the genome more directly related to fitness. In a similar way, although unique alleles do not necessarily reflect adaptation, they may, if numerous or at high frequency, provide an indication of likely adaptive differences elsewhere in the genome.

Several types of genetic analyses can provide information relevant to ESA considerations. Gene diversity analysis (Nei, 1973) can be used to partition the total genetic variance in a species in a variety of ways, including between-population, within-population, and between-years (within population) components. Results can be compared to data for other species (and other salmonids in particular) to provide insight into the degree of genetic distinctness of the population under consideration. Genetic distance indices can be used in a similar fashion, and comparisons of heterozygosity levels may also be informative in some cases.

Phenotypic and life history traits may reflect local adaptations, and for this reason they may be relevant to the evaluation of population distinctness. However, expression of these traits is known to be affected by environmental as well as genetic factors (Barlow, 1961; Clayton, 1981), which complicates their interpretation. Sorting out the genetic and environmental effects on phenotypic and life history characteristics is a challenging task and has been a central focus in evolutionary biology (Endler, 1986).

Analysis of habitat characteristics is important in two ways. First, the existence of unusual or distinctive habitat features allows for the possibility of unique adaptations in the local population. Second, identification of unusual or distinctive habitat is one step toward achieving the broad purpose of the Act—to preserve threatened and endangered "species" and the ecosystems they inhabit. Again, however, caution should be used in drawing inferences based on physical characteristics of the habitat without supporting biological information linking the habitat differences to adaptations. Just as our perception of what constitutes a barrier to fish migration can be faulty, so too our understanding of the importance of various habitat characteristics to organisms is far from complete.

Recommended Approach

The following two-step approach is suggested for making a determination regarding population distinctness under the Act.

1) Evaluate the degree of reproductive isolation. If there is gene flow with other populations, it should be at a level low enough to permit evolutionarily important divergence. If apparent migration rates with adjacent populations are high, the population would not be considered isolated unless there is evidence that the genetically effective migration rate is much lower. Approaches outlined in the previous section on "Reproductive Isolation" should be used to address the questions of migration rate, gene flow, and recolonization rate.

If the population is believed to be reproductively isolated, an evaluation under step 2 (below) should be made; if it is not isolated, the population is not an ESU and should not be considered a separate "species" under the Act (presumably, however, it would be part of a larger unit that is an ESU).

2) Evaluate evidence for ecological/genetic distinctness in the context of similar data from throughout the species range, as well as for other species as appropriate. Often, this process will involve difficult judgments concerning the relative importance to attach to different types of evidence. Although a variety of approaches may prove useful in making this determination, none will provide a completely objective assessment of evolutionary significance. Nevertheless, some general guidelines can be suggested to aid the evaluation process.

The existence of substantial genetic differences from other conspecific populations based on protein electrophoresis or DNA analyses would strongly suggest that evolutionarily important, adaptive differences also exist[7]. The failure to find such differences (or the absence of genetic data) would not rule out the possibility that such adaptive differences exist, but it would place a greater burden of proof on data for other characters. Data for habitat characteristics should be interpreted in a similar fashion: habitat dif-

[7] Although protein electrophoresis and DNA techniques are considered together here for convenience, a variety of parts of the nuclear or mitochondrial genome can be targeted for genetic study. Sensitivity of the different approaches can vary considerably, and this factor must be considered in interpreting the results of genetic analysis.

ferences suggest (but do not prove) the possibility of adaptive differences, whereas the inability to detect habitat differences constrains the scope of possible local adaptations but does not prove they do not exist. In evaluating data for phenotypic and life-history traits, every effort should be made to account for environmental effects that are manifested in periods shorter than one generation (and therefore do not reflect adaptations).

Special Considerations

Anadromy/Nonanadromy

Some species of Pacific salmon, *Oncorhynchus nerka*, *O. mykiss*, *O. clarki*, and perhaps others, have nonanadromous as well as anadromous forms that occur together. A similar phenomenon occurs in some species of the genera *Salmo* and *Salvelinus*. This raises the question whether the two forms should be considered jointly or separately in deciding if a population is "distinct" under the Act. The following general guidelines are suggested.

The two forms should be considered separately if they are reproductively isolated. As noted above, the question of reproductive isolation is likely to be one of degree. Again, the key question is whether isolation is strong enough for evolutionarily important differences to develop in the two forms. Data from protein electrophoresis or DNA analyses can be valuable in making this determination, as can observations of time and place of spawning and behavioral interactions during spawning. Information from other populations (and other species) can help provide a context for making the evaluation. However, such studies suggest that a variety of scenarios probably exists in nature, from substantial reproductive isolation of sympatric anadromous and nonanadromous forms to substantial life-history plasticity within presumably a single gene pool (Foote et al., 1989; Kirpichnikov et al., 1990). Therefore, such studies are unlikely to provide an unequivocal answer for an unstudied anadromous/nonanadromous system.

If substantial gene flow occurs or has recently occurred between the two forms, they represent polymorphisms within a single population and should be considered as a unit for purposes of the Act. In determining whether such a population unit is an ESU, the anadromous and nonanadromous traits should be considered in the same manner as other population characteristics discussed in the section on "Ecological/Genetic Diversity." The important questions are whether the traits have a genetic basis and whether they help to make the population unit "distinct" from other populations. For example, an anadromous/nonanadromous unit might be considered an ESU if other ecologically comparable populations of the species harbored only the nonanadromous form. In this case, if the population unit is considered to be an ESU solely or primarily on the basis of the anadromous trait, then the potential loss of anadromy should be a legitimate ESA concern. A key question would be whether the nonanadromous form was likely to give rise to the anadromous form after the latter had gone locally extinct. Therefore, an anadromous/nonanadromous population unit could be listed based on a threat to one of the life-history traits, if the trait were genetically based and loss of the trait would compromise the "distinctness" of the population.

Differences in Run-time

In several species of Pacific salmon, biologists recognize different run-times, or races, of fish inhabiting the same general area. Generally, run-times are determined on the basis of the time of year at which adults enter fresh water to spawn; in some cases, fish with different run-timing also have different juvenile life history patterns (Healey, 1983; Groot and Margolis, 1991). The question whether such races represent "distinct" populations under the Act can be addressed in the framework developed above.

First, it should be determined whether the different run-times are reproductively isolated. Often, the formal distinction between run-times is rather arbitrary, with (for example) fish appearing before a certain date classified as "springs" and those appearing after that date as "summers." Races that are arbitrarily defined in this fashion may in fact be reproductively isolated, but if so this needs to be demonstrated biologically (for example, by providing evidence for a discrete distribution of run-times or distinct times and/or locations of spawning).

Assuming that fish with different run-times are reproductively isolated, they can be considered distinct populations under the Act if they exhibit evolutionarily important ecological/genetic differences, as outlined in the section on "Ecological/Genetic Diversity." In the absence of substantial isolation between run-times (or if the races are reproductively isolated but do not individually satisfy the ecological/genetic diversity criterion), a "population" unit consisting of two or more recognized run-times could be considered an ESU if it were isolated from and distinct from other populations.

Hatchery Fish

Artificial propagation has been used in one form or another with anadromous Pacific salmon for over a century. Hatcheries have been used both for fisheries enhancement (largely as mitigation for losses of native stocks caused by destruction of habitat or blockage of migratory routes) and in an attempt to boost production of naturally-spawning fish (Lichatowich and McIntyre, 1987). Currently, hatchery operations in the Pacific Northwest are carried out on a large scale, and the majority of adult fish produced in many systems are of hatchery origin (Washington, 1985; Vreeland, 1986). It is important, therefore, to consider the role that hatchery fish play in ESA considerations for Pacific salmon.

The Act (Sec. 3(3)) identifies "propagation" as one method that may be used to conserve threatened or endangered species, and both NMFS and FWS have used captive breeding or other artificial propagation techniques with listed "species," including several fishes. Artificial propagation may thus be an appropriate tool for use in recovery plans for some "species" of Pacific salmon. However, the Act also mandates conservation of native ecosystems "upon which endangered species and threatened species depend." The key here is the link between threatened and endangered species and their native ecosystems; the link may be jeopardized if either component (the species or the ecosystem) is emphasized to the exclusion of the other. Because a

fish hatchery is not a substitute for a natural ecosystem, maintaining a "species" in a hatchery while allowing degradation of its native habitat is not consistent with the stated purposes of the Act. For this reason, attention in ESA evaluations of Pacific salmon should focus on fish that spend their entire life cycle in their native habitat—i.e., those that are progeny of naturally spawning parents. Such fish will be referred to as "natural" in the ESA context[8]. Threshold determinations also will focus on natural fish, on the premise that an ESU is not healthy unless a viable population exists in the natural habitat.

Once the natural component of a population has been identified, the next step is to determine whether this population component is "distinct" for purposes of the Act. In making this determination, the twofold criteria for defining an ESU should be used. If it is thought that artificial propagation may have affected the genetic composition of the natural population (either directly through supplementation or indirectly through straying of hatchery fish), factors outlined in the following section should be considered. Fish are not excluded from ESA consideration simply because some of their direct ancestors may have spent time in a fish hatchery. However, there are a number of potential genetic consequences of artificial propagation that should be considered in this context. Thus, fish meeting the definition of "natural" adopted here may subsequently be excluded from ESA consideration for other reasons.

In developing recovery plans for "species" listed as threatened or endangered, the use of artificial propagation may be considered. If a hatchery is associated with the listed "species," an important question to address in formulating a recovery plan is whether the hatchery population is similar enough to the natural population that it can be considered part of the ESU defined on the basis of that natural population. Factors to consider in this regard are discussed in the next section. Given various uncertainties, it should generally be presumed that hatchery fish are not part of an ESU unless there is a compelling reason for including them.

Effects of Artificial Propagation and Other Human Activities

Two possible effects of artificial propagation are of particular concern in ESA evaluations: 1) Genetic changes within a population and 2) mixtures of genetically distinct populations. These effects should be evaluated from the perspectives of both the hatchery population(s) involved and any natural population that may have been affected. That is, an evaluation of the nature and extent of these effects will help to determine 1) whether a natural population is an ESU and 2) whether a hatchery population(s) should be included in an ESU defined on the basis of a distinct natural population.

Supplementation (the release of hatchery-reared fish into habitat occupied by fish of the same biological species), transfer of eggs or fish among hatcheries, and unintentional straying are all aspects of artificial propagation that can lead to population mixing. Such mixing is relevant to the question of population distinctness because a population that has been overplanted with fish of different origin may not be an ESU even if it once was distinct. Similarly, a hatchery stock that has resulted from extensive transfers of exogenous fish is unlikely to be part of an ESU.

Apart from the effects of stock mixtures, artificial propagation can also lead to either random or directional genetic change within cultured populations. Random genetic changes, if of sufficient magnitude, may lead to the erosion of genetic variability and may overwhelm selection for locally adapted genotypes, thus reducing fitness. Directional genetic change can occur at the time of founding a hatchery population (or between generations in a hatchery) through choice of which individuals will be allowed to reproduce. In addition, fish hatcheries differ from the natural environment in a number of ways that may affect selective pressures experienced by the population.

Determinations regarding the distinctness of populations that may have been affected by artificial propagation should be consistent with the twofold criteria that define an ESU. In making this determination, it may be useful to consider whether the population was likely to have been an ESU in the past and to ask whether stock mixing (or other aspects of artificial propagation) has compromised the evolutionarily important adaptations that distinguished the original population. Several factors should be considered in this context. (It is assumed that the population in question was distinct enough to be an ESU prior to the effects of human activities.)

First, although stock transfers of anadromous Pacific salmon have been widespread in the past (Withler, 1982), evidence merely of the release of exogenous fish is not sufficient to disqualify a population from consideration as an ESU. Stock transfers (or straying) have a direct genetic effect only if the transplanted fish successfully reproduce and contribute to subsequent generations of the native stock. Results of supplementation efforts with Pacific salmon have been quite variable (Ricker, 1972) and at present are largely unpredictable. For example, a recent review of salmonid studies (Hindar et al., 1991) cited examples in which the native stock had been largely or entirely displaced, examples of hybridization between native and introduced fish, and examples in which repeated hatchery releases had no detectable genetic effect on the native population. Therefore, it should not automatically be assumed that transplantation efforts have permanently altered the genetic structure of native populations; similarly, some stock transfers among hatcheries may not have permanent genetic effects.

Second, a population that does not represent a completely pure native gene pool may still qualify as an ESU if it is adapted to its local environment and is "distinct" by the criteria outlined in the section "Application to Pacific Salmon." This point is important for Pacific salmon, because there are relatively few populations for which the possibility of some genetic influence from transplants or hatchery strays can be completely excluded. How much introgression from other gene pools must occur before a population no longer merits consideration as an ESU depends to some extent on

[8] This corresponds to the usage suggested by Bjornn and Steward (1990); some other authors have used the term in a different way.

the degree of distinctness of the original population.

In evaluating the effects of population mixture, the following types of information should be gathered whenever possible:

1) Genetic, phenotypic, and life history traits and habitat characteristics for all stocks involved;
2) Broodstock and rearing protocols for all relevant stocks;
3) Dates of release, number released, and developmental stage at release for transplanted stocks (or those involved in straying);
4) Trends in abundance of the local population for a time span bracketing the periods(s) of release (or straying events); and
5) Evidence for reproductive success of transplanted (or stray) fish, including evidence for incorporation of foreign genes into the local population.

Ideally, information will be available for the transferred stock as well as for the local stock both before and after the mixture event(s). This type of data would allow an evaluation of whether changes in the local stock are in the direction predicted under the assumption that the mixing has had a permanent effect. In practice, such extensive data will not always be available, and in this event the evaluation can be much more difficult. Nevertheless, there are some approaches (Waples and Smouse, 1990) that have reasonable power to detect population mixtures under certain conditions.

Finally, although genetic changes within cultured populations are a legitimate ESA concern, the effects of such changes on the viability of natural populations of anadromous salmonids are largely unknown. Random changes occur in all populations, at a rate inversely proportional to the effective population size. Unless the number of spawners is severely limited, random changes can generally be minimized in cultured populations by following appropriate broodstock practices (Meffe, 1986; Simon et al., 1986; Allendorf and Ryman, 1987). This has not always been the case with fish hatcheries, however. Allendorf and Ryman (1987) reviewed a number of studies of cultured populations of trout and Atlantic salmon that provide evidence for severe inbreeding depression and/or substantial loss of genetic variation. Such dramatic effects have not been documented with Pacific salmon, but there is indirect evidence (Waples and Teel, 1990) that effective population size in some hatcheries is small enough that such problems are a potential concern.

For populations under ESA consideration, the importance of random changes attributable to a history of artificial propagation can be evaluated by examining the number and sex of spawners each year, methods of fertilization, and rearing protocols. Exports of eggs or progeny offsite should also be considered; if (as has often occurred in the past) the entire production of certain families is shipped to another hatchery, those families do not contribute to the effective size of the local population (Simon et al., 1986). In addition, the variability among individuals in reproductive success is a key factor in determining effective population size, but this parameter is very difficult to measure for Pacific salmon. For this reason, a monitoring program that uses indirect genetic methods (Waples, 1990b) can provide useful insights into the magnitude of random genetic changes.

Directional genetic changes can occur from a variety of factors. The practice of culling fish according to age, time of return, size, or appearance was formerly widespread in Pacific salmon hatcheries (Donaldson and Menasveta, 1961). More recent awareness of the drawbacks to this approach can help to minimize such effects, but they cannot be eliminated entirely. In addition, anadromous fish hatcheries, if successful in their goal of ensuring that a large proportion of progeny survive to time of release, also dramatically alter the mortality pattern for the population. In general, this can be expected to lead to genetic change relative to a population that spawns naturally (Waples, 1991b). Furthermore, a number of characteristics of the hatchery environment—both physical (e.g., substrate type, water temperature and flow, and the variability of same) and biological (e.g., density, food type and source, behavioral interactions, incidence of predators)—differ so markedly from the natural environment that selective changes are likely.

Unfortunately, it is easier to identify the potential genetic risks posed by artificial propagation than to evaluate their actual impact on a given population. As a general principle, it is probably fair to say that genetic changes in a population that result from adaptation to hatchery conditions are unlikely to increase the fitness of the population in the natural environment. How rapidly such effects occur, however, and whether they are reversible are open questions at present.

Some idea of the likely magnitude of selective changes due to artificial propagation can be gained by considering past hatchery practices for the stock in question and the number of generations in culture. If possible, baseline data from the original (prehatchery influence) population should be compared to data from the current population. Focus should be on 1) possible reductions in the ability of the population to survive and reproduce in the natural environment, and 2) possible changes in characteristics that help to make the population distinct. Again, genetic changes within cultured populations are important to consider from the perspective both of the hatchery population (and its relation to an ESU) and any natural populations that may have been affected by the cultured stock.

Other human activities (e.g., fishing, habitat degradation) can also alter the genetic structure of native populations, and the importance of these factors to ESA considerations can be evaluated in a similar way. For example, fishing pressure can selectively affect certain size or age groups (Ricker, 1981; Nelson and Soule, 1987), and these characteristics may be heritable. The relevant question is whether the activities have changed the population so much that it no longer represents an evolutionarily significant component of the biological species.

Introduced Populations

In general, populations resulting from the introduction of fish into a local area not occupied by the biological species (particularly if the area is outside the historic range of the species) are probably not ESU's because they do not contrib-

ute to maintaining diversity of the species in its native habitats. Again, the key is the link between a "species" and its native habitat, and this link is broken when fish are moved from one ecosystem to another. Some introduced populations should not be excluded from ESA consideration, and these include populations occupying habitat that is ecologically similar and geographically proximate to the source population, and those that represent the only remaining component of a native gene pool. In the former case, the introduced population may be determined to be part of the same ESU as the parent population; in the latter case, the population could be determined to be an ESU if it met the criteria outlined in the section "Application to Pacific Salmon."

Historic Population Size

For a population that once was abundant but since has declined in numbers, there should be no minimum size for ESA consideration. However, populations may also be small because of limiting physical or biological factors. For Pacific salmon, suitable habitat may severely limit the potential number of spawners and hence the carrying capacity of small streams. Given the large temporal fluctuations in abundance documented for every species (and many populations) of Pacific salmon, and given the likelihood that even greater fluctuations have occurred over evolutionary time, there must be some size below which a spawning population is unlikely to persist in isolation for a long period of time. The fact that small spawning aggregations are regularly observed may reflect a dynamic process of extinction, straying, and recolonization. Such small populations are unlikely to be ESU's, although a collection of them might be. Therefore, the historic size[9] of a population may be useful in evaluating whether it is an ESU.

Both genetic and demographic factors should be considered in making this evaluation. Although there is no consensus among geneticists regarding the minimum effective population size per generation (N_e) necessary to avoid long-term problems of inbreeding and loss of genetic variability, most estimates are in the range of several hundred (see discussions by Lande and Barrowclough (1987) and Simberloff (1988)). For a species with overlapping age classes and an average age at spawning of 3-5 years (typical of many populations of steelhead and chinook, chum, and sockeye salmon), this would correspond to an effective number of breeders per year (N_b) of perhaps 50-100. (Waples (1990a) provides a discussion of the rate of loss of genetic variability in Pacific salmon and the relationship between N_e and N_b.) Because not all individuals successfully spawn, and because the variance among individuals in reproductive success may be high, the total number of adults must generally be somewhat more than this (perhaps several times as many). The long-term persistence of an isolated population also depends on its ability to withstand inevitable (and often large) fluctuations in abundance caused by the interplay of population dynamics, changing environmental conditions, and chance events. The importance of these factors varies among species and among populations within species and must be evaluated on a case-by-case basis. In general, however, such fluctuations may place greater constraints on the long-term survival of small populations than do genetic factors associated with inbreeding.

A Pacific salmon population should not be considered an ESU if the historic size (or historic carrying capacity) is too small for it to be plausible to assume the population has remained isolated over an evolutionarily important time period. In making this evaluation, the possibility should be considered that small populations observed at present are still in existence precisely because they have evolved mechanisms for persisting at low abundance. Population genetics theory indicates that gradual inbreeding over a period of time may purge deleterious, recessive alleles from a population, lessening the effects of inbreeding depression and allowing a smaller effective size than would ordinarily be the case. It is possible that, in some populations, a similar process—evolution of demographic parameters, for example—may have occurred that modulates the effects of environmental variability. Because such populations would contain adaptations that might truly be considered to be of evolutionary significance to the species, and because small populations in general are a likely source of evolutionary innovation, it is prudent to exercise caution in eliminating a population from ESA consideration simply on the basis of historic size. In particular, theoretical considerations about the likely persistence time of small populations should not override strong evidence for long-term reproductive isolation. Nevertheless, this concept should prove useful in focusing attention on population units with the greatest probability of representing ESU's.

Groups of Populations

As anadromous species, Pacific salmon spawn in a freshwater environment that is often naturally organized in a hierarchical fashion: Major river systems may contain several large tributaries, each with numerous streams fed by smaller creeks, etc. Other areas may be characterized by numerous smaller streams, each entering directly into a tidewater area. In both cases, geographic, environmental, or other factors may naturally lead to genetic structuring of the various spawning aggregations into more or less discrete units. The first step in determining the appropriate hierarchical level for consideration as an ESU is to identify units within which levels of gene flow are high relative to the rate of exchange between units. Often, however, there will be more than one hierarchical level for which this is true. Therefore, it is important to identify reproductively isolated units that also contribute substantially to ecological/genetic diversity of the species as a whole.

Determining the appropriate level for consideration as an ESU is a challenging task with Pacific salmon. Although the strong homing instinct of these species indicates that even small spawning aggregations may potentially represent

[9] This concept is related to, but differs from, the concept of minimum viable population size (MVP) (Shaffer, 1981; Soule, 1987). The MVP concept considers the future and asks how large a population must be to have an acceptably high probability of surviving a specified period of time. The historic population size concept considers the past and asks how small a population must be before it becomes unreasonable to assume it has persisted in isolation long enough for important adaptations to evolve.

biological populations, such populations may not meet the criteria to be considered "distinct" under the Act. A group of populations, however, might be distinct from, and isolated from, other groups of populations. Such a group of populations can constitute an ESU and, if determined to be threatened or endangered, can be afforded protection under the Act.

In evaluating the appropriate grouping level, a balance must be struck between two opposing concerns. On the one hand, it is important to identify the smallest units that meet the criteria set out in the section on "Application to Pacific Salmon," because this allows the greatest flexibility in ensuring the appropriate level of protection for different ESU's within a more comprehensive group. On the other hand, we have seen in the previous section, "Historic Population Size," that the smallest units supporting local populations of salmon may not be evolutionarily independent from other nearby populations. A key question is: How can evolutionarily important units be protected without running the risk of attempting to artificially maintain units that might naturally undergo episodes of extinction/recolonization on something short of evolutionary time scales?

The following approach is suggested. Identifiable ESU's should not be combined for the sake of convenience. In general, however, ESU's should correspond to more comprehensive units unless there is clear evidence that evolutionarily important differences exist between smaller population segments. This approach is consistent with the recommendation that NMFS and FWS should use sparingly their authority to list vertebrate populations, and only if biological evidence clearly warrants it. In addition, this approach reflects 1) the view that population "distinctness" should be supported by positive scientific evidence and 2) the concern that fragmenting groups of populations into multiple ESU's on the basis of insufficient data may create artificial units without a biological basis.

Nevertheless, it is recognized that the long-term viability of a larger unit may also depend on the continued existence of multiple, semi-independent units it comprises. Fragmentation or gradual loss of habitat can pose a threat to larger population units. The underlying concern should be whether important genetic resources of the biological species are at risk because of the fragmentation. If so, then the appropriate action may be to protect the larger population as a whole, rather than the individual fragments. In this context, NMFS recognizes that thresholds for threatened and endangered status must be flexible enough to deal with threats to groups of populations (metapopulations) and clinal populations as well as more discrete population units. Just as there is no simple formula for determining evolutionary significance, there is no universally applicable numerical threshold for a listing determination; in both types of evaluation, a variety of factors must be considered. Recovery plans for listed "species" could take this into account by ensuring protection for smaller units within a more comprehensive ESU. This might be appropriate, for example, if the smaller units differ in various characteristics but it is uncertain how these differences relate to evolutionary significance.

Interpreting Results of Statistical Tests

Sampling Considerations

Rigorous analyses of data used in ESA considerations will include testing hypotheses whenever possible, and sampling protocols are important to consider in this context. In general, regardless of the characters being considered, the appropriate null hypothesis to test is that no differences exist between the populations being compared. Sampling from the populations introduces a source of random error with magnitude inversely proportional to sample size. In many statistical tests, the implicit assumption behind the null hypothesis is that the samples being compared were randomly drawn from the same population. There are several ways in which this basic assumption might be violated by the method of sampling, and the effects of violating the assumption are often magnified in small populations (as may frequently be encountered in ESA evaluations). Furthermore, the unusual life history features of Pacific salmon (in particular, the combination of overlapping age classes with one-time reproduction) provide some additional opportunities for sampling bias. These factors should be kept in mind in designing sampling plans and in evaluating results.

Temporal changes within populations. Although most Pacific salmon spend the majority of their life at sea, they exist in recognizably discrete populations only during rearing as juveniles and spawning as adults. By necessity, samples are generally taken from local spawning populations, and often only a single brood year is sampled. It must be realized that the population as a whole includes several brood years, and values for a given character will show year-to-year variation around the mean for the population as a whole. The effects of temporal variation within a population must be considered in comparing single-brood-year samples from different populations; in general, this factor will inflate the observed level of difference above that predicted by the null hypothesis, even if the overall population means do not differ (see discussion of a similar point in Waples and Teel (1990)). A study plan that involves temporally spaced samples within sites as well as samples from geographically distinct localities is the best way to evaluate the significance and stability of between-population differences.

Life history stage sampled. Waples and Teel (1990) showed that, in comparing two (or more) samples, the probability of a statistically significant result may depend on the life history stage sampled. In general, sampling juveniles will tend to produce larger differences (and a higher probability of a significant test result) than sampling adults. This will be a minor effect if the sample size is small relative to the population size, but this will not always be true for populations under ESA consideration.

Nonrepresentative sampling. Most statistical tests assume random sampling, which means that every individual in the population(s) has an equal opportunity to appear in the sample. There are several ways in which this condition might not be met with Pacific salmon. For example,

adults may be sampled during only part of the spawning run, or only in limited areas of a stream. Under certain circumstances, samples of juveniles may include large numbers of individuals from the same family. Methods for sampling either life history stage may select for certain types of individuals.

Significance of Results

It is important to realize that "statistical significance" is a different concept than "evolutionary significance" as it relates to the Act. In the present context, a statistically significant result indicates that the means for a pair or group of samples differ by more than would reasonably be expected if a single population were sampled repeatedly. The conclusion, then, would be that the population means are different for the character under consideration. Being "different," however, is not the same as being "distinct" under the Act. For a population to be considered an ESU, it must differ from other populations in an evolutionarily important way. Statistical tests can be useful in making this determination but do not in themselves provide direct evidence regarding evolutionary significance. Similarly, failure to find a statistically significant difference does not disprove the existence of population differences. Power to detect true differences in population means is a function of sample size, so this factor should also be considered in evaluating results of statistical tests.

General Comments

This paper presents a simple, flexible framework for interpreting language in the Endangered Species Act pertaining to vertebrate populations: Simple because a pair of criteria can be applied to determine whether a population segment is distinct and hence a "species" for purposes of the Act, and flexible because the two criteria can be used to address a variety of issues of particular concern for Pacific salmon.

By focusing on evolutionary significance, the ESU concept also provides a means of dealing with several recurring problems posed by the term "distinct population segment." For example, in 1979 the GAO pointed out potential abuses in the authority to list vertebrate populations, suggesting that this could lead to absurdities such as the listing of squirrels in a specific city park[2]. Such a result is unlikely under the present framework. Although squirrels in a park might at present be effectively isolated from squirrels in other parks or natural habitat, such a population would be unlikely to meet the second criterion for an ESU (evolutionary significance). Similarly, a population unit recently isolated as a result of human activity (by the construction of a dam, for example) probably also does not meet the second criterion, because most of the diversity presumably would be retained in the larger source population. The same might be true for some natural isolates, particularly those of recent origin.

Many will have noted that although this paper establishes a framework for considering populations of Pacific salmon under the Act and provides guidance for its application, it does not provide a simple formula for determining whether the unit under consideration is a "species." To the extent that the process would be simpler and more objective with such a formula, the approach adopted here is a disadvantage. However, use of a simple (or even a complex) formula does not seem consistent with the stipulation of the Act to make decisions "solely on the basis of the best scientific and commercial data available." The process of evolution and differentiation within and between species is manifest in so many different ways that no simple yardstick will be universally applicable. Ryder (1986:10) came to essentially the same conclusion regarding the difficulties in identifying important conservation units within mammalian species:

"Identification of ESU's within a species was recognized as a difficult task, requiring the use of natural history information, morphometrics, range and distribution data, as well as protein electrophoresis, cytogenetic analysis, and restriction mapping of nuclear and mitochondrial DNA."

Acknowledgments

This paper has drawn heavily on several sources. First, the paper by Utter (1981) laid a solid foundation to build upon, and many of the ideas expressed in that earlier paper appear here in similar form. Second, NMFS solicited public comments on a summary of the 1981 paper, and a number of those suggestions, including ideas discussed at ESA Technical Committee meetings, have been incorporated into the present document. Third, many of the concepts outlined here were discussed in one form or another at the FWS-NMFS Vertebrate Population Workshop held in Washington, D.C., in June 1990. The goal of the workshop was to develop a consistent approach for determining whether vertebrate populations are "distinct" under the Act. In particular, I want to acknowledge Andrew Dizon (NMFS, La Jolla, Calif.) for introducing the ESU concept and Mark Shaffer (FWS, Washington, D.C.) for stressing the importance of considering ecological and habitat characteristics. Fourth, public comments on the NMFS Interim Policy and accompanying technical paper were useful in preparing this revised document. Finally, a number of people within NMFS and FWS and the NMFS Peer Review Group critically reviewed drafts of the manuscript, and Pat Montanio (NMFS, Silver Spring, Md.) and Karl Gleaves (Office of NOAA General Counsel, Silver Spring, Md.) provided valuable guidance relating to the legislative and legal history of the Endangered Species Act.

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Biographic Memoir of Ernest Ingersoll: Naturalist, Shellfish Scientist, and Author

CLYDE L. MacKENZIE, Jr.

Introduction

The name Ernest Ingersoll is well-known to many shellfishery biologists as the author of two outstanding monographs on the shellfisheries of the United States and Canada in the 1880's. The first (Ingersoll, 1881a), entitled "A Report on the Oyster-Industry of the United States," was a 252-page description of historical and contemporary oyster fishing, marketing methods, and statistical data in the eastern provinces of Canada and the coastal states of the United States. The second (Ingersoll, 1887), entitled "The Oyster, Scallop, Clam, Mussel, and Abalone Industries," was a 120-page summary of the first monograph about oysters as well as a history and description of contemporary methods and statistical data of the other shellfisheries. Although Ingersoll was, by profession, a naturalist and author but only briefly a shellfish scientist, these monographs are regarded as benchmarks, providing the principal descriptions of shellfisheries in North America in the 1700's and 1800's.

Early Life

Ernest Ingersoll was born in Monroe, Mich., on 13 March 1852, the son of Timothy D. Ingersoll, a dental surgeon and writer on dental topics, and Eliza (Parkinson) Ingersoll. Like many naturalists of that era, his principal amusement as a boy was searching through the woods and fields around Monroe for rare and curious natural history specimens. In 1867, he entered Oberlin College, Ohio where he studied science and was curator of the college museum; he was graduated in 1871. From the fall of 1872 to the spring of 1874, he was a student assistant in the Museum of Comparative Zoology at Harvard University, helping with collections of birds and mammals (Avery, 1926; *The New York Times*, 1946). The museum was founded and administered by Professor Louis Agassiz, the eminent teacher-naturalist. Ingersoll attended zoology classes at the Lawrence Scientific School (Harvard University) and spent the summer of 1873 as a student of Professor Agassiz at his seaside school on Penikese Island, near Woods Hole, Massachusetts (Ingersoll, 1933).

Clyde L. MacKenzie, Jr., is with the Sandy Hook Laboratory, Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Highlands, NJ 07732.

Western Expeditions

The death of Agassiz in 1873 led Ingersoll indirectly into journalism, when he wrote a sketch of Agassiz containing some highlights of his teachings and submitted it to *The New York Tribune*. The editor published it immediately in January 1874 (no day available) and sent Ingersoll a check for $40 with a note asking him to write more articles of scientific interest (Ingersoll, 1933). He did so the following year, after accepting a position as a zoologist with the expedition of Dr. Ferdinand V. Hayden of the United States Geological and Geographical Survey of the Territories, then working in Colorado (Fig. 1).

The expedition's mission was to describe the topography, geology, and natural history of the West. Ingersoll was assigned to the Photographic Division, under the leadership of William Henry Jackson. Jackson's photographs during this and later expeditions were to make him famous, and he and Ingersoll became life-long friends (*The New York Times*, 1946). Ingersoll (1875) published a paper on his zoological survey entitled, "Report on the natural history of the United States Geological Survey of the Territories, 1874", summarizing his collections and identifications of freshwater invertebrates, mainly mollusks.

While on this expedition, Ingersoll and Jackson were the first trained scientists to see and describe the Mesa Verde ruins in southwest Colorado, cliff dwellings of an ancient Indian civilization (Fig. 2) (*The New York Times*, 1946). First news of their finding reached the East through Ingersoll's dispatches in columns of *The New York Tribune* in the summer of 1874. The finding created wide interest, especially among anthropologists. When the expedition reached its home base at Colorado Springs, Colo., Ingersoll found a telegram from the *Tribune* editor, offering him a job.

As a reporter to the *Tribune*, he covered mainly religious camp meetings in and around New York City (Ingersoll, 1933). From 1875 to 1877, he also was natural history editor of a magazine called *Forest and Stream and Rod and Gun* (forerunner to *Field and Stream*), and contributed articles to it as well as to other periodicals.

In 1877 Ingersoll made a second trip to the West, camping for 3 months in Wyoming, Idaho, and other relatively undeveloped regions. He contributed articles to *Forest and Stream and Rod and Gun*, *Harper's*, and *Scribner's* magazines and *The New York Herald* on his observations. In 1878-79 he was on the editorial staff of *Science News*. In 1879 the Century Company hired him to visit Colorado and write an article about frontier and mining life there (*The New York Times*, 1946).

The Shellfishery Monographs

In 1879 Ingersoll also began his U.S. shellfishery surveys (Fig. 3). His monographs were part of a series, written as a joint enterprise between the U.S. Fish Commission and the Census Bureau. The intent of these agencies was to describe comprehensively the methods of the fisheries, the distribution of the fishing grounds, and the natural history of commercial marine animals. G. Brown Goode, Assistant Director of the National Museum, organized and directed the preparation of the monographs. Twenty-two agents, one of whom was Ingersoll, then only in his late 20's, conducted the field investigations (Baird, 1884). (Goode had already been engaged for a number of years in a systematic, historical, and statistical investigation of American fisheries.)

An office staff supported Goode's field agents. It handled correspondence, searched past records, and helped prepare the reports of the field agents for publication. The Census Bureau paid for the field work, while the Fish Commission paid for the preparation of the monographs (Baird, 1884).

Ingersoll may have been chosen to write the shellfishery monographs because he had demonstrated experience in observing various areas in the West. The techniques he had used in covering topography and animals (including mollusks), using interviews of settlers and Indians to learn about their histories and way of life, and writing about them, were the same as would be needed to survey the shellfisheries and prepare the two monographs. His experiences as a reporter and editor were useful also. Ingersoll worked 22 months on the project, from 1 October 1879 to 1 July 1881.

Ingersoll's monographs (1881a, 1887) have importance because they are the only good histories and documentation of shellfishing practices prior to 1900. They related that many people were employed in shellfishing, and shellfish were common in people's diets in coastal North America in the 1800's. The monographs were typical of Ingersoll's writings as they included all available pertinent information, interesting historical perspectives, overviews, and vivid images with sometimes humorous details and statistics of subjects previously overlooked by other writers. Ingersoll based each of his publications on thorough field and library research. He wrote well, in a clear and lively style.

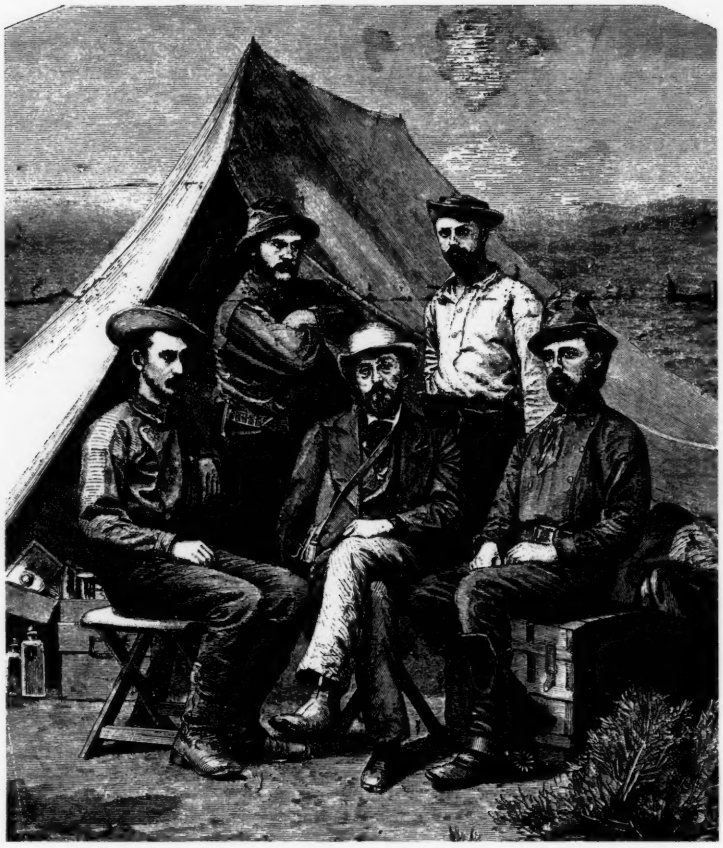

Figure 1.—Five members of Ferdinand V. Hayden's exploring expedition in Colorado. Ernest Ingersoll, Zoologist, is standing at right, Ferdinand V. Hayden, Geologist-in-Charge, is seated in the center, and William Henry Jackson, Photographer, is seated at right. The illustration is autographed by Ingersoll and Jackson. Source of photograph: Library of Explorers Club, New York City.

Extensive Travels

Ingersoll studied the shellfisheries from the Maritime Provinces of Canada to Texas by travelling along shorelines and visiting ports and marketing cities. He also reported on the oyster industry of California using information from another investigator. He described the local beds, boats and gear, and daily and annual landings, as well as pertinent regulatory legislation, and collected statistics, some of which he had to estimate. For vignettes and shellfishery histories, he interviewed local authorities and fishermen and collected documents. His on-site visits and interviews gave his reporting strong credibility. In the 1800's, pollution of shellfish beds was not a major concern since the only polluted areas were adjacent to cities, such as New York. People were interested in predators which limited shellfish

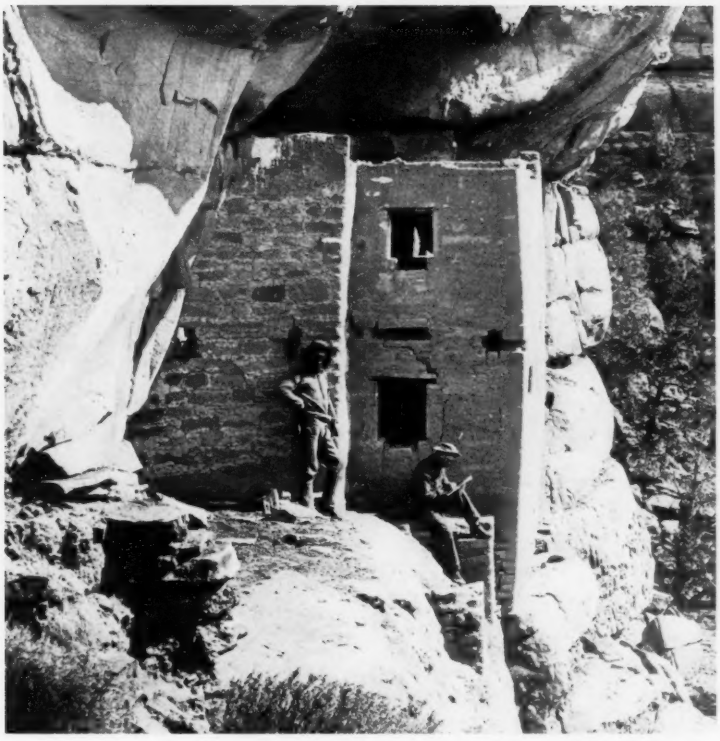

Figure 2.— Mesa Verde dwellings in Colorado, photographed by William Henry Jackson, when he and Ernest Ingersoll discovered them in 1874. Ingersoll is sitting and recording his observations beside the dwellings. Source of photograph: Museum of New Mexico, Santa Fe.

Figure 3.—Portrait of Ernest Ingersoll at the age of 26 in 1878, the year before he began his shellfishery surveys. Source of photograph: Linnaean Society of New York, New York City.

abundances, and thus his monographs included discussions of control measures for drum-fish, *Pogonias cromis*; oyster drills, *Urosalpinx cinerea*; and starfish, *Asterias forbesi*.

Ingersoll (1881a) wrote that the earliest explorers of North America had observed Indians eating a variety of shellfish. On Atlantic shores, Indians ate oysters, blue mussels, horse mussels, razor clams, cockles, bay scallops, and hard clams, as well as freshwater unios and anodonts, and left large shell-heaps (middens). Along the Gulf coast, Indians left shell-heaps of many shellfishes, and along the Pacific Coast they left shell-heaps mostly of mussels. He recorded that they also left shell-heaps of freshwater mussels and clams along the banks of a number of rivers, including the Mississippi, Ohio, Susquehanna, Delaware, Merrimac, and Concord. Ingersoll mentioned that shell-heaps were worldwide in distribution. For example, the shores of Denmark and Norway had ancient shell-heaps up to 300 m long, 60 m wide and 3 m deep. They were the midden heaps of ancient mollusk eaters and contained blackened stones, indicating fireplaces, and fragments of animal bones, rude utensils, and implements.

Chesapeake Bay Oysters

Chesapeake Bay was the largest producer of oysters for direct consumption and as a source of seed for more northern planters. In 1880 Chesapeake Bay produced some 17 million bushels of oysters and about 40,000 people were employed in that industry. In the early to mid 1800's, when the supply of native oysters in northern estuaries failed to meet the demand, planters from Massachusetts, Narragansett Bay, Rhode Island, Long Island Sound, Raritan Bay (New York and New Jersey), and Delaware Bay sailed schooners and sloops to Chesapeake Bay to purchase seed for replanting beds in their waters. The captains bought oysters from tongers in Maryland and Virginia. When the vessels arrived at their destinations, additional men reinforced their crews and using six-tine forks they shovelled the cargos of 2,500-5,000 bushels of oysters onto beds. The quantities were impressive. From 1850 to 1860, planters imported 100,000-150,000 bushels annually to Wellfleet, Mass. In 1880 planters imported about 450,000 bushels to Narragansett Bay, 450,000 bushels to Long Island Sound, 300,000 bushels to Raritan Bay, and 700,000-800,000 bushels to Delaware Bay. They harvested the

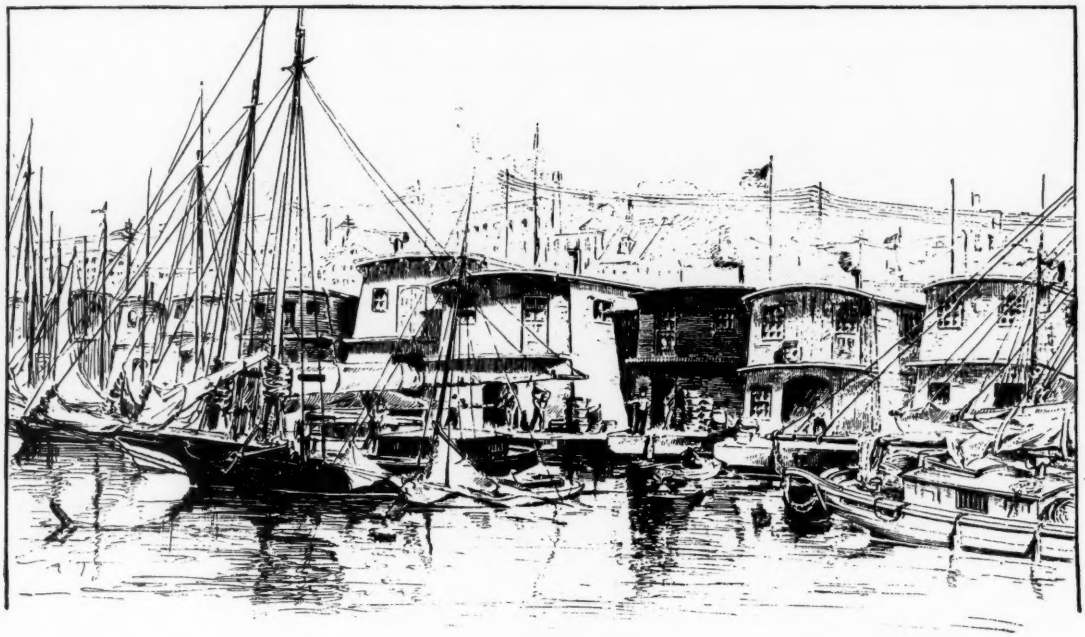

Figure 4.—Figure from Ingersoll (1881a) entitled "Oyster barges at the foot of West Tenth Street, North River, New York City."

oysters and sold them to various oyster markets the succeeding fall.

Oyster Markets

One of the largest markets for oysters was New York City (Fig. 4), where they were enjoyed by rich and poor alike. The city was the principal market for oysters grown from Norwalk, Conn. to the mid-coast of New Jersey. Ingersoll (1881a) wrote: "Oysters were pickled, stewed, baked, roasted, fried, and scalloped; oysters were made into soups, patties, and puddings; oysters with condiments and without condiments; oysters for breakfast, dinner, and supper; oysters without stint or limit, fresh as the pure air, and almost as abundant, are daily offered to the palates of the Manhattanese, and appreciated with all the gratitude which a bounty of nature ought to inspire."

The largest oyster market on the east coast, and probably in the world, was Baltimore. During the season from 1 September 1879 to 15 May 1880, fishermen brought 7 million bushels of oysters to Baltimore for local consumption or packing and subsequent shipment.

Soft and Hard Clams

Ingersoll wrote that soft clams occurred from the Maritime Provinces to Virginia. Fishermen gathered them with iron rakes. One of the largest producing states was Maine where 318,383 bushels were dug in 1879; cod and mackerel fishermen purchased 90 percent of them for bait. Those used as food were eaten by the fishermen (who were also farmers), local villagers, or by people who came down from the interior, as Indians had done, to enjoy a feast of clams and seaside recreation. Fishermen also sold some in local markets. In 1880 total landings of soft clams along the east coast of North America were about 1 million bushels.

Ingersoll stated that quahogs (hard clams) were abundant from Cape Cod to Florida, the largest supply coming from bays on the south shore of Long Island. In Great South Bay, Long Island, fishermen raked and tonged quahogs throughout the year, but mostly in summer when oysters were not in season. The number of diggers totalled 500 men and 200 boys. In good days, each dug about 3 bushels of quahogs which sold for a total of $2. Buyers shipped most to New York City and sold the remainder to hotels on the island. In 1880 total landings of quahogs along the east coast were about the same as for soft clams, just over 1 million bushels as recorded by Ingersoll. The following two paragraphs from his 1887 monograph are examples of the human touches Ingersoll frequently included in his publications.

He wrote: "A 'clam-bake' expresses the sum of all human happiness to the Rhode Islander, and to gather all his relatives and friends on the sea-shore, bake the roystering clam in dried seaweed, and eat it with other good things, fills his cup of joy. As enthusiasm and emotion always seem odd, and perhaps ludicrous to those who are not under its influence, the New Englanders get much fun poked at them by outsiders. It is related, for example, that a Sunday-school teacher in Rhode Island told the

pupils that there were poor children in Illinois who had never experienced the supreme delight of a clam-bake, and the last penny in the juvenile pocket was dropped in the plate in aid of the benighted sufferers."

Bay Scallops

Ingersoll stated that fishermen gathered bay scallops by towing small, triangular dredges from rowboats or sailboats. The scallops were opened at the shore, commonly by women. Some young wives opened scallops by hand "... with cradles behind them containing less than year-old babies... singing merrily some baby song to quiet the young ones, and by an indescribable motion of the left foot rocking the cradles with a gentle motion all-sufficient to keep the nurseling quiet. In another corner was a mother nursing her three-weeks-old babe at an interval in the work."

Mussels, though abundant, were not consumed to any extent, according to Ingersoll. Farmers used some for fertilizer.

Since the early 1900's, oyster production has declined sharply. The principal causes of the decline were the ready availability of beef and poultry (which sharply reduced the demand for oysters), pollution of beds rendering some oysters inedible, and diseases which caused large mortalities of oysters. On the other hand, people increasingly eat mussels now. Farms in eastern Canada and Maine grow most of them.

Later Writings

Following his shellfish survey work, Ingersoll spent his summers from 1882 to 1887 touring wilderness areas of the western United States and Canada and writing books and articles about his travels. He also worked as editor of *Manhattan Magazine* during 1883-84. Part of the time he worked for the Canadian Pacific Railway, writing guidebooks and other travel-related publications for it, thus acting as the first press agent for a railroad (Schwarz and Schlaikjer, 1947). In 1887 and 1888, while continuing this work, he lived in Montreal, but afterward moved to New York City (Avery, 1926).

Ingersoll wrote about 20 books during the late 1800's and early 1900's. Some of them include: "Nests and Eggs of American Birds" (1880), "Friends Worth Knowing: Glimpses of American Natural History" (1881b), "Birds Nesting" (1882), "Knocking 'Round the Rockies" (1883), "The Crest of the Continent" (1885), "Down East Latch-Strings" (1887), "Wild Neighbors" (1897), "Gold Fields of the Klondike and the Wonders of Alaska" (1897), "The Book of the Ocean" (1898), "Nature's Calendar" (1900), "Wild Life of Orchard and Field" (1902), "The Wit of the Wild" (1906), "The Life of Animals The Mammals" (1907), and "Zoology; the Science of Life" (1922).

Ingersoll's articles about the outdoors, Indian life and Indian-Caucasian interactions, fur trading, bears, beavers, buffalo, and similar topics appeared in a variety of magazines, journals, and newspapers over the years. Besides the monographs on shellfisheries, his publications related to fisheries included: "A short lecture on fishes" (1877); "On the fish-mortality in the Gulf of Mexico" ([1881] 1882), the first published account of fish mortalities caused by red tides in Florida; "Wampum and its history" (1883); "Mollusks in general" (1884); "Natural history of economic mollusks of the United States" (1884); a chapter entitled, "Fishing and other marine industries" in "The Book of the Ocean" (1898); and a chapter entitled, 'Catching menhaden off Montauk' in "Wit of the Wild" (1906). Considered as one of the eminent naturalists of his period, Ingersoll was invited to serve as editor and submit contributions to the Standard Dictionary, New International Dictionary, Encyclopedia Americana (*The New York Times*, November 14, 1946), and The Standard Library of Natural History (Published by The University Society of New York in 1908).

One of the literary banes of the late 1800's and early 1900's was "Nature-faking" (guessing about or embellishing the natural history of wild animals and plants and publishing the results), but it was never a pitfall to Ingersoll. He wrote only about what he had observed or considered accurate in the literature. When President Theodore Roosevelt severely criticized "nature-fakers" in a published interview, he mentioned Ingersoll as a writer whose accuracy was exemplary. Afterward, Roosevelt invited him to the White House for a luncheon and the two became friends. In 1907 the President appointed him head of the Oyster Commission in Washington (Schwarz and Schlaikjer, 1947) (no record was found of his duties or length of service in this position). Among his other friends were the famous naturalists William Beebe and John Burroughs.

Environmental Protection Urged

Ingersoll was one of the early advocates of the protection of natural habitats and wildlife in the United States. In lectures delivered in the late 1800's to nature and women's clubs in the midwest under the auspices of the University of Chicago, he stated that all life in a given region is interconnected so that disturbance of any part disarranges the whole. He urged each person to protect natural habitats and also desist from the pleasure killing of wild animals. In a lecture presented in about 1888, Ingersoll (N.d., ca. 1888) said: "I believe that every person should regard himself as a trustee of nature for the benefit of his fellows and posterity; and that the wanton destruction of animal life is a sin against nature, against heaven and against humanity. I believe that the man or woman who commits that sin should be looked upon with such stern disfavor as that which society metes out to those who transgress the laws of the land." He stated that a well-filled notebook was worth more than boxes of dead specimens, photographs were worth more than stuffed animals in a museum, and education about enjoying the activity of life and beauty of animals should begin at childhood. He also stated that man could have prevented much of the destruction of natural areas and animal life, as he moved westward across the United States, through wise planning (Ingersoll, N.d., ca. 1888). Moreover, he was an excellent speaker. His lectures were highly instructive and interesting, holding the attention even of children who attended them (according to reports in the Galesburg, Illinois *Register* and Newark, Ohio *Tribune* on file at Mus. Nat. Hist., N.Y.).

From the early 1890's to about 1905, Ingersoll worked part-time for Rand,

McNally, and Co., researching, writing, and updating illustrated guidebooks. They described New York State, the Hudson River and Catskill Mountains, New York City, the New England states, Washington, D.C., and the southwestern states.

From 1900 to 1938 Ingersoll lived in New York City and wrote a weekly column for a Montreal newspaper, *The Family Herald and Star Weekly* (Fig. 5). The newspaper sought to increase its readership by including a column devoted to natural history and hired Ingersoll, a well-known authority and a proven, capable writer on such subjects, to write it. His column, titled "The Natural History Club," reached about a half million people a week throughout Canada and the Caribbean. It consisted of answers to readers' inquiries and presentations of new information about nature. From readers' letters, it became apparent that birds were the object of most interest and, at the time, a good identification guide, particularly for western birds, was lacking. Thus Ingersoll prepared a classification list of nearly all of the birds of Canada, giving a description of each species. This emphasis on birds ran for more than a year and was of great benefit to Canadian naturalists. Another notable service was a detailed review of eastern Canadian snakes (12 articles), illustrated and partly written by Ingersoll's only surviving child, a daughter, Helen, who also illustrated some of his books. Other articles featured insects, salamanders, and turtles and the farming of deer, foxes, frogs, marten, and mink. The readers of the newspaper regarded Ingersoll as a great oracle and sage about nature (*The Family Herald and Weekly Star*, October 14, 1925; *The New York Tribune*, March 11, 1932).

Ingersoll was a member of several prestigious organizations in New York City. He was one of two founders of the Linnaean Society of New York (naturalists, systematists, and zoologists) in 1878 and was its first secretary (Schwarz and Schlaikjer, 1947); he was elected a fellow of the Society on its 50th anniversity in 1928. He was a member of the National Association of Audubon Societies and the New York Zoological Society. He was also a member of the Authors Club

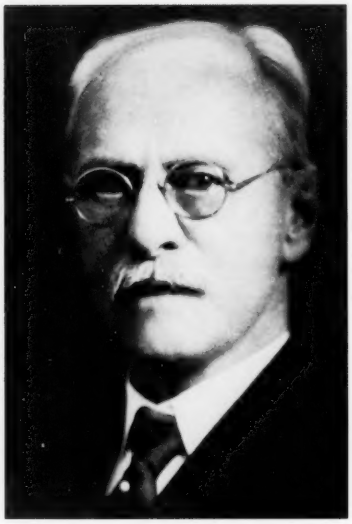

Figure 5.—Portrait of Ernest Ingersoll at about 65 years of age. Source of photograph: Library of Explorers Club, New York City.

(critics, dramatists, journalists, novelists, and poets; about 250 members), and was its secretary from 1920 to 1925; a member of the Barnard Club (authors, bankers, diplomats, lawyers, and painters; about 650 members), and the Salmagundi Club (architects, engravers, illustrators, painters, and sculptors) from 1916 to 1937. He was present at the founding of the Explorers Club in 1905 and was a member thereafter; he was its director and secretary for many years and editor of its quarterly magazine, *The Explorers Journal*, from 1926 to 1931. He was, in effect, a real Renaissance man.

Ingersoll retired from writing his newspaper column in 1938 when he was 86 years old, ending a career that lasted a full 65 years. He died in a nursing home in Brattleboro, Vt., on 13 November 1946 at the age of 94 (Schwarz and Schlaikjer, 1947).

Ernest Ingersoll spent his career following one of the tenets of his most-admired mentor, Louis Agassiz. The latter taught his students that their mission in life should be to make science popular and interesting to the public, and if they did that it would be a blessing to the country (Ingersoll, 1933). The care which Ingersoll took with his writings, his many publications, and the subject matter he chose all demonstrate that he cared a great deal for his fellow man and the natural world. Ingersoll never mentioned his shellfishery surveys and monographs for the U.S. Fish Commission and the Census Bureau in his later writings. Perhaps he did not realize how valuable they would come to be to future generations of shellfishery biologists.

Acknowledgments

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The Status of Loggerhead, *Caretta caretta*; Kemp's Ridley, *Lepidochelys kempi*; and Green, *Chelonia mydas*, Sea Turtles in U.S. Waters: A Reconsideration

Assessing the status of widely distributed marine species can prove difficult because virtually every sampling technique has assumptions, limitations, and biases that affect the results of the study. These biases often are overlooked when the biological and nonbiological implications of the results are discussed. In a recent review, Thompson (1988) used mostly unpublished population census data derived from studies conducted by the National Marine Fisheries Service (NMFS) to draw conclusions about the status of Kemp's ridley, *Lepidochelys kempi*; Atlantic coast green turtles, *Chelonia mydas*; and the loggerhead sea turtle, *Caretta caretta*.

We briefly critique Thompson's data and conclusions with respect to the presentation of incorrect information, inadequate citation of pertinent published literature, reliance on unpublished and nonpeer-reviewed reports to assess population size and status, and development of conclusions that do not follow from the data. The point of this letter is not to criticize the need to review data but rather to point out that many of the assumptions and techniques discussed by Thompson (1988) have not been evaluated in the peer-reviewed literature.

The limitations of aerial survey techniques to estimate population size in murky Atlantic waters have never been rigorously examined. For example, Marsh and Saalfeld (1989) were unable to identify individual sea turtle species during aerial surveys of clear waters of the Australian Great Barrier Reef. Attempts to standardize data for perception and availability biases were not successful. How would perception and availability biases influence population assessment in offshore waters of the southeastern United States where visibility is poorer?

One of our primary concerns is the reliance on unpublished information to support statements about status or population size. Thompson ignored published research and in so doing missed the opportunity to make comparisons among studies. For example, aerial surveys of the Gulf Stream and inshore waters of the Atlantic Ocean and Gulf of Mexico were conducted prior to the surveys mentioned by Thompson (Hoffman and Fritts, 1982; Fritts et al., 1983). By ignoring references, the review disregarded the contributions of other researchers. In some cases, published research by NMFS biologists was not mentioned, e.g., Schroeder and Thompson (1987). A second concern is that assumptions were not justified beyond references to unpublished reports. Thompson stated that the mean number of loggerhead turtles present during the peak spring/summer survey from North Carolina to Key West was 387,594 (95% C.I. $\pm$ 20,154). She does not acknowledge any limitations in applying radio-telemetry data obtained in one spatially limited study (at Canaveral Ship Channel, Fla.) to determine the below-surface turtle numbers over the entire area from North Carolina to Key West. We cannot determine from data whether extrapolation between studies is behaviorally or temporally justified, Other information (Byles, 1988; Byles and Dodd, 1989) suggests that the amount of time loggerheads spend at the surface varies greatly with activity, temperature, depth, and season.

Thompson derived independent loggerhead mortality estimates for the Atlantic Ocean and Gulf of Mexico by multiplying the published (no citation given) value of turtle catch per 1,000 pounds of shrimp landed by the total amount of the shrimp catch. In neither case was the geographical limits of the estimate given. The assumption is that mortality can be estimated despite nonrandom spatial and seasonal sampling using experimental excluder trawl surveys, observers on shrimp vessels, and "intermittent 1973-78 shrimp discard observations." We suspect that the standard errors of such estimates may be large although there is no way to tell. There seems little justification for Thompson's contention that there have been between 10,000 and 23,000 turtles killed yearly since 1973. Henwood and Stuntz (1987) estimated that approximately 10,000 sea turtles died from shrimp trawling based on data gathered in 1983, although they did not extrapolate their findings to other years. Henwood and Stuntz (1987) provided a sound rationale and basis for the derivation of a mortality estimate. If Thompson applied Henwood and Stuntz' (1987) methodology to data from other years, why not say so? If she didn't, how were her mortality figures derived?

When assessing the "status of stocks" of loggerheads, various figures were provided without an adequate explanation as to how the figures were derived or whether underlying assumptions were valid. The survivorship requirements assumed that 387,000 loggerheads constitute a "unit stock." The assessment assumed a mortality figure of 10,000-23,000 per year during shrimp trawling. According to Thompson, between 0.8% and 5.2% of hatchlings entering the water must survive to maintain population stability. Although often cited, a hatchling survivorship value of 1% to maintain a stable population has no basis in empirical data (Frazer, 1986, 1987). Such estimates were derived from theoretical considerations and are based on assumptions, such as a stationary population, that may not be valid for today's turtle populations (Frazer, 1986).

Thompson claimed the number of nesting females and the number of turtles in the water indicated a stable population since 1980, but gave no supporting data. In contrast, the long-term studies in coastal Georgia indicate an overall 3% annual decline in the number of nesting females since the early 1970's (Frazer, 1983, 1986). Over the past few years, the decline has been much greater, approaching 9% (J. Richardson, personal commun.). Similar declines are occuring in South Carolina. Considering the increased development and disruption of nesting beaches and the continued heavy shrimping activity undertaken until recently without Turtle Excluder Devices (TED's), we believe it unlikely that offshore sea turtle populations have not been impacted. If "we do not have an adequate data base to evaluate these [population estimate of 387,000 plus likely detrimental impacts from shrimping] conflicting effects on the population dynamics of this species" (p. 19), it

would seem impossible to conclude that "there is no apparent risk of major declines over the next 10 years."

Contrary to Thompson's assertion that no historical records of green turtle nesting in the United States are available, Dodd (1982) summarized nesting records in Florida and first suggested that the population might be increasing. Significant references to the turtle fishery in Florida (Witzell, 1987) and Texas (Doughty, 1984) were overlooked, as were citations to the original literature on which much of the discussion in this section was based. And while the spatial limits of the Florida population cannot be ascertained at present, the results of Bowen et al. (1989) suggest that the population is more "closed" than Thompson states. Although small green turtles will accept animal matter in captivity and the nutritional habits and requirements of wild adults and juveniles are reasonably well known (Mortimer, 1981; Bjorndal, 1985), there is no basis to say that green turtles pass through an omnivorous dietary stage, or that this transition occurs at age 3.

Estimating time to extinction in long-lived animals is fraught with model assumptions and should not be presented without thorough discussion. Thompson's estimate of 208 years for the nesting population of *L. kempi* to become extinct is difficult to accept because a minimum viable population size has never been established for the species. Thompson contradicts herself by stating on p. 22 that the Rancho Nuevo population will be extinct in 208 years if a 3% population decline continues and then stating on page 23 that 100 nesting females will remain in 2196 at the same rate of decline.

Biologists reviewing complex and often contradictory information face dilemmas about the extent of coverage a review should give, whether to use data not generally available to colleagues, and space limitations. These factors may have influenced Thompson's (1988) review. However, important background and supporting information should not have been omitted. We believe that the status of these species has received superficial coverage. Several reviews of biological data now have been published (Dodd, 1982, 1988; Ehrhart and Raymond, 1987; Ross et al., 1989) on these species which give a better picture of their status in U.S. waters. Future reviews should focus on the need for publication in peer-reviewed journals with clear presentation of techniques, assumptions, and results which follow from the data. Accepting estimates of population size, mortality, and trends are not justified until these conditions are met.

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C. Kenneth Dodd, Jr.
National Ecology Research Center
U.S. Fish and Wildlife Service
412 N.E. 16th Ave., Room 250
Gainesville, FL 32601

Richard Byles
Division of Endangered Species
U.S. Fish and Wildlife Service
P.O. Box 1306
Albuquerque, NM 87103

A Response to Dodd and Byles

Dodds and Byles (1991) raise several questions regarding the quality of the data and validity of the conclusions presented in my review paper (Thompson, 1988). As a point of reference, this paper was the result of a collaborative effort in 1986 with myself, and T. A. Henwood and W. E. Stuntz who subsequently and independently published their estimates of turtle mortality from offshore commercial shrimp trawling (Henwood and Stuntz 1987; Thompson, Henwood and Stuntz 1986[1]). Since that time, as Dodd and Byles (1991) note, there have been several review publications which include new information on the status of sea turtles in U.S. waters (Dodd, 1988; Hopkins-Murphy and Murphy, 1988; Ross et al., 1989; Marquez, 1990; Magnuson et al., 1990). Herein, I will address

[1] Thompson, N. B., T. Henwood, and W. E. Stuntz. 1986. A summary of information on three species of marine turtles in U.S. waters. Coast. Fish. Resour. Div., Miami Lab., SEFC, NMFS, Contrib. ML1-86-57, 35 p.

the most critical concerns, in my opinion, of Dodd and Byles (1991).

The value of pelagic aerial surveys to derive a synoptic index of abundance for marine turtles has been debated over the past 13 years or so since this technique was first applied by the University of Rhode Island (CeTAP, 1982). The CeTAP report (1982) describes the pelagic aerial and vessel effort to census cetaceans and turtles in North Atlantic waters off the northeast U.S. coast. While statistically evaluating the CeTAP marine turtle data, Thompson and Shoop[2] (1981) concluded that the aerial survey approach was appropriate to count large loggerhead and leatherback turtles at the surface of the water. Our results[2] formed the basis of the NMFS surveys of the North Atlantic off the southeast U.S. coast and reported by me. Notably, the sampling design and preliminary results from our surveys were reviewed at the First and Second Stock Assessment Workshops held at the NMFS Southeast Fisheries Center, Miami, Fla., in August 1982 and 1984, respectively (Powers, 1983; Powers, 1985). These workshops convened scientists inside and outside of NMFS to review stock assessment information and evaluate the research which provided this information for fishery and protected resources under the purview of the NMFS Southeast Fisheries Center. Since the first stock assessment workshop, results of our surveys have been regularly presented (Thompson, 1983; Thompson, 1984a, b; Schroeder and Thompson, 1987).

More recently, our data were provided to the National Academy of Sciences and selected data are included in Appendix D of the Committee on Sea Turtle Conservation Report (Magnuson et al., 1990). Magnuson et al. (1990) concluded that aerial survey data were indeed "valuable for surveying large areas . . ." A variety of environmental factors will bias results, and many of these were examined statistically by Thompson and Shoop[2], re-examined by Powers (1983) and reiterated by Magnuson et al. (1990). The major problem in converting surface counts to total abundance via density estimation is applying a conversion factor to account for turtles under the water's surface. Stratification of this factor by species, size class, time, and space was noted in Powers (1983) and again pointed out by Dodd and Byles (1991). However, the consistent application of the best available estimate for this species within the sampling area and closest to the aerial survey sampling period was applied to our survey results (Powers, 1983). Unfortunately, Dodd and Byles (1991) offer no alternative to this methodology to census turtles in the water over a large area, which would provide a productive exchange.

I am particularly concerned about the criticism of the use of NMFS excluder trawl survey data, shrimp vessel observer data, and intermittent shrimp discard observation data. These were the data utilized by Henwood and Stuntz (1987) to estimate turtle mortalities and the basis for the National Marine Fisheries Service Turtle Excluder Device (TED) regulations (50 CFR Parts 217, 222, and 227 Sea Turtle Conservation; Shrimp Trawling Requirements; Final Rule, Federal Register, Vol. 52. No. 124, Monday, June 29, 1987, p. 24244-24262). These data on the incidental catch of turtles in commercial offshore shrimp trawls were also provided to Magnuson et al. (1990) who concluded that Henwood and Stuntz (1987) may have underestimated mortality attributable to offshore commercial shrimp trawling. Notably, I developed an independent estimate of shrimp trawl related mortality which is slightly higher than that of Henwood and Stuntz (1987). The purpose of this second analysis to estimate shrimp trawl mortalities was to underscore the validity of that of Henwood and Stuntz (1987) (Thompson et al.[1]). These independent estimates represent the "best available information" which form the basis for the subsequent analysis on stability conditions for the loggerhead turtle (Thompson and Powers 1986[3]). Apparently, I credit the reader in understanding the assumptions and limitations of this approach. It is only an attempt to determine the future of this species over the short term (10 years), does not imply that turtles have not been negatively impacted by shrimp trawling or any other anthropogenic cause of mortality, and represents a first step in evaluating a large body of data available on this species. In my opinion, the debate on the validity of our turtle mortality estimates from commercial shrimp trawling has been laid to rest. I do not believe that Dodd and Byles (1991) are interested in resurrecting this debate.

The question on the definition of stocks, particularly as it pertains to the green turtle, remains a subject of debate (Powers, 1983). It is hard to believe that any species such as the green turtle, that has persisted so long, does not demonstrate some movement between "populations." In the absence of stock boundary data, I advocated a management approach that favors the turtles; that total protection is still needed to effect recovery (Thompson, 1988).

I do not understand the contradiction that Dodd and Byles (1991) point out with my assessment of the status of the Kemp's ridleys. I identified some period of time to real extinction (zero females) vs. some rate to functional extinction (100 females). The point here is that under the conditions for the period 1978 through 1987, the index used to evaluate the status of this species, the number of nesting females at Rancho Nuevo, continued to decline. Under unchanging conditions, annual decline is expected. With the full implementation of the TED regulations, the conditions current in 1988, no longer exist. As an optimist, I believe this bodes well for the recovery of this species.

Quite honestly, one motive for pursuing publication of my overview paper was to provide some incentive to others to publish their information on the status of sea turtle stocks in U.S. waters. A regularly conducted assessment of the status of these populations is the only way we will be able to know how well we are doing in recovering these species. This means that evaluating the best information may alter previous conclusions. I am optimistic that the publication of

[2] Statistical analyses of sea turtles: Data derived from the 1979 Cetacean and Turtle Assessment Program. Univ. R.I., Kingston, Contr. NA-81-FA-C-000011, 33 p.

[3] Thompson, N. B., and J. E. Powers. 1987. An assessment of the status of the loggerhead turtle (*Caretta caretta*) in the U.S. Natl. Mar. Fish. Serv., Southeast Fish. Cent., Miami, Fla. Unpubl. manuscr.

information on the status of these stocks will continue. This is absolutely critical to the survival of these species.

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Nancy B. Thompson
Miami Laboratory
Southeast Fisheries Science Center
National Marine Fisheries Service
NOAA, 75 Virginia Beach Dr.
Miami FL 33149

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